Climate Change and Future Forests of the Boundary Waters Canoe Area Wilderness: An Assessment of Temperate Tree Abundance, Earthworm Invasion and Understory Regeneration Trends

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I would also like to thank Dr. Paul Bolstad, Dr. Rebecca Montgomery, and Dr. Peter Reich for their support as both learned professors and insightful committee members.

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To Melissa and Will.
Thank you for your unwavering love and support.
Let’s go to the cabin now.

Non scholae sed vitae discimus

ABSTRACT

The forests of the Boundary Waters Canoe Area Wilderness (BWCAW) are dominated by boreal tree species at their southern range limit, making them particularly sensitive to climate change. Numerous studies have modeled potential climate change induced tree species range shifts across northern Minnesota and the BWCAW, projecting declines for boreal tree species and increases for northern temperate tree species currently at low abundances in the wilderness. The coarse resolution of these models, their lack of some biological interactions and the unprecedented velocity of projected future climate change could lead to over and/or under estimates of tree species range shifts at the scale of the BWCAW. To better understand potential forest successional shifts within this ecologically important wilderness we assessed 1) the abundance and spatial distribution of northern temperate tree species, 2) the stage, pattern, and extent of earthworm invasion in the wilderness, and 3) the impact of seasonal temperature, overstory composition, earthworm invasion and soil moisture potential on the understory relative density of ten boreal and northern temperate tree species. We found that red maple (*Acer rubrum)* is the most abundant temperate tree species in the BWCAW by orders of magnitude across all size classes, with its spatial distribution strongly correlated with an existing west to east summer temperature gradient. Conversely, our results raise questions about whether adequate seed sources of other temperate species are currently present in the wilderness to support a successful boreal to temperate transition. Earthworm invasion in the BWCAW is widespread, yet incomplete. Modeling results indicate the spatial pattern of earthworm invasion in the wilderness is driven by anglers dumping unused earthworm fishing bait at campsites. We predict that 33% of total land area in the BWCAW is currently invaded by earthworms. Lastly, our results indicate that summer temperature is a key driver of differences in understory relative density of boreal and northern temperate tree species across the mixed-boreal forests of the BWCAW, but that earthworm invasion and areas with increased soil moisture availability may support the short-term resistance of boreal tree species under future warmer and drier conditions.

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Introduction

European earthworms have become a key driver of ecological change in previously earthworm-free northern temperate and boreal forests of North America (Bohlen et al. 2004a, b; Frelich et al. 2006). Earthworms are ecosystem engineers capable of modifying the physical, geochemical and biological properties of forest soils (Jones et al. 1994; Bohlen et al. 2004a). Earthworm invasion into forests that have developed in the absence of these keystone detritivores leads to profound changes in soil structure, most notably the elimination of the forest floor, and a significant increase in soil bulk density (Hale et al. 2005; Frelich et al. 2006). This physical reengineering of forest soils leads to changes in fundamental ecological processes including nutrient cycling, hydrology and seedbed conditions, which can trigger a cascade of deleterious effects on native biodiversity and influence forest compositional shifts in response to climate change (Frelich et al. 2006; Holdsworth et al. 2007; Frelich and Reich 2009; Craven et al. 2017).

There are no native earthworms in the western Great Lakes region of central North America, as any native species were most likely extirpated by the Wisconsin glaciation (James 2004). Researchers estimate that European earthworms have invaded approximately 80% of forests in Minnesota and Wisconsin to varying degrees (Holdsworth et al. 2007; Hale 2008). The initial origins of this invasion have been traced back to the arrival of early European settlers, but its current widespread extent is a relatively recent development over the last several decades, driven in large part by

anglers dumping their unused earthworm fishing bait at cabins, resorts, boat launches and other angling-related sites throughout the lake-filled region (Reynolds 1977; Gates 1982; Alban and Berry 1994; Proulx 2003; Holdsworth 2007). Beaver tails (*Lumbricus rubellus)* and nightcrawlers (*Lumbricus terrestris)* are the two most common species of earthworms sold as fishing bait (Keller et al. 2007). They are also the two most common and ecologically damaging earthworm species currently invading western Great Lakes forests (Holdsworth et al. 2007).

Northern temperate forests that have developed in the absence of earthworms build up a thick, yet permeable forest floor (organic, or O horizon) that retains soil moisture, modulates soil temperature, favors plant species that germinate in leaf litter, serves as an important rooting and nutrient cycling zone and provides habitat for a host of native plant and animal species (Bormann and Likens, 1979). Upon invasion, earthworms consume the forest floor, replacing it with a dense and compacted bare mineral soil surface that is warmer and drier during the growing season, and often with reduced nutrient availability (Hale et al. 2005). In maple (*Acer)* dominated forests, invasions by beaver tails and nightcrawlers have led to reductions in native plant diversity and abundance (Gundale 2002; Hale et al. 2006; Holdsworth et al. 2007), extirpation of rare native plants (Gundale 2002), declines in woodland salamander and arthropod abundance (Migge-Kleian et al. 2006; Maerz et al. 2009), and reduced nest survival of a ground-dwelling songbird (Loss and Blair, 2011).

In addition to their direct impacts on understory biodiversity, earthworms are also expected to influence forest compositional shifts within the temperate-boreal ecotone in response to climate change (Fisichelli et al. 2012). The bare and compacted mineral soil

surface created by earthworms increases evaporative losses of soil moisture and decreases infiltration of precipitation (Frelich et al. 2006). Combined with increasing temperatures, this creates warmer and drier soils that favor drought tolerant species able to germinate on bare mineral soil (Eisenhauer et al. 2011). These conditions strongly disfavor sugar maple (*Acer saccharum),* possibly creating a competitive advantage for other temperate species including red maple (*Acer rubrum)* and northern red oak (*Quercus rubra)* (Frelich et al 2012). Because all boreal tree species are able to germinate on bare mineral soil, and deer preferentially browse temperate tree seedlings over boreal seedlings, some researchers have concluded that earthworms may delay the migration of temperate trees northward while favoring boreal tree species resistance due to reduced competition (Fisichelli et al. 2012; Frelich et al. 2012; Fisichelli et al. 2013). However, in a recent microcosm study, nightcrawlers reduced germination rates of boreal tree species including balsam fir (*Abies balsamea)*, white spruce *(Picea glauca),* black spruce (*Picea mariana)* and jack pine *(Pinus banksiana),* and reduced survival rates of balsam fir and white spruce seedlings (Drouin et al. 2014). Earthworms have also been shown to facilitate invasion by nonnative, invasive plants including buckthorn (*Rhamnus cathartica),* which could benefit from the dynamic and novel successional conditions created by a changing climate, earthworm invasion and a host of interrelated drivers of change within the temperate-boreal ecotone (Nuzzo et al. 2009; Roth et al. 2015).

The Boundary Waters Canoe Area Wilderness (BWCAW) in northeastern Minnesota is particularly vulnerable to earthworm invasion and the associated ecological impacts. The BWCAW is a popular fishing destination and earthworms are a preferred type of live bait on wilderness canoe trips due to their relative ease of transport. An

important biodiversity refuge, 69 species of greatest conservation need in Minnesota are known or predicted to occur within its borders, which contain some of the largest tracts of unlogged forest in the eastern United States (Frelich 1995; Heinselman 1996; MN DNR 2006). Although not fully boreal, forests in the BWCAW are nevertheless dominated by boreal tree species near their southern range limits, making them particularly sensitive to climate change and the compounding effects of earthworm invasion (Frelich and Reich, 2009).

Despite these factors, we know very little about the current extent, stage and pattern of earthworm invasion within the BWCAW. Most studies of earthworm invasion in the western Great Lakes region have occurred in relatively accessible, maple-dominated hardwood stands as these forests are particularly vulnerable due to a high proportion of calcium-rich leaf litter preferred by earthworms and many decades of multiple human uses (Gundale 2002; Gundale et al. 2005; Hale et al. 2005; Reich 2005; Holdsworth et al. 2007; Costello & Lamberti 2008; Loss & Blair 2011; Shartell et al. 2013). To our knowledge, there have been no published studies of earthworm invasion in the BWCAW, nor in the surrounding northern conifer forests of the western Great Lakes region. And we are aware of just one study of earthworm invasion in a recreational boreal wilderness area as expansive and remote as the BWCAW, where lower levels of development, and different patterns of human use and travel could influence the relative importance of potential introduction sites as well as the species most likely to be introduced (Saltmarsh et. al. 2016). There are however, a growing number of studies documenting active earthworm invasions in boreal forests across Canada, and evidence that boreal deciduous leaf litter is able to support large populations of beaver tails and

nightcrawlers (Ferguson 2004; Cameron et al 2007; Eisenhauer 2007; Cameron and Bayne 2009; Addison 2009; Moore et al 2009; Cameron and Bayne 2012; Sanderson et al 2012; Cameron et al 2015). These factors highlight a clear need for a baseline understanding of earthworm invasion in the BWCAW.

The purpose of this research was to assess the stage, pattern, and extent of earthworm invasion in the BWCAW to better understand potential impacts on understory biodiversity and forest successional shifts under climate change. Stage of invasion was classified on a five-point scale with the number and types of earthworms, as well as their ecological impact, increasing from stage one (presumed earthworm free) to stage five (fully invaded). Pattern of invasion was defined as the spatial relationship between the probability of earthworm invasion at different stages and a suite of predictor variables associated with potential introduction sites and earthworm habitat suitability. A more detailed description of invasion stage and invasion pattern predictor variables can be found in the methods section. Extent of invasion was defined as the percentage of land area within the BWCAW predicted to be currently invaded across different stages of invasion.

We hypothesized that the probability of more advanced stages of invasion would be positively related to proximity to likely bait-dumping sites, namely campsites and portage trails, and areas with higher availability of temperate and boreal deciduous leaf litter. Conversely, we expected increases in slope and elevation, both of which could pose physical impediments to the introduction and natural spread of earthworms on this bedrock-dominated terrain, to be negatively related. Finally, we hypothesized that invasion fronts would be widespread given decades of fishing pressure and a high

number of potential bait-dumping sites spread throughout the wilderness, but that invasion extent would be lower than other studies in the Western Great Lakes region due to the relative inaccessibility of a large portion of the BWCAW and a higher proportion of conifer tree species producing litter types less preferred by earthworms.

Study area

The BWCAW is a 400,000 ha, federal Wilderness area located within the Superior National Forest in far northeastern Minnesota, USA. Its forests have been described as "near boreal," with fires of varying intensity and frequency creating a patchwork of pure and mixed stands of boreal species including jack pine, black spruce, balsam fir, quaking aspen (*Populus tremuloides)* and paper birch (*Betula papyrifera).* Red pine (*Pinus resinosa)* and eastern white pine (*Pinus strobus)* stands are often found on leeward lakeshores and islands where fire intensity was typically less, and stands of northern white cedar (*Thuja occidentalis)* are often found on wet sites (Frelich & Reich 1995; Heinselman 1996). Some northern temperate species are also present in the Wilderness, primarily red maple and northern red oak, with some stands found on the western side where summer temperatures are on average 2°C warmer (Ohmann & Ream 1971; Heinselman 1996; author unpublished data). While logging is currently prohibited in the BWCAW, approximately 50% of the area within its current borders was logged between the 1890s and the late 1970s (Heinselman 1996).

The entire BWCAW is underlain by Pre-Cambrian rock, primarily granite but also gabbro, greenstone and some slates. Its soils are the result of sandy and gravelly loam glacial deposits, and soils are generally thin with rocky outcroppings and exposed bedrock common along lakeshores and on ridge tops (Ohmann & Ream 1971). Glacial

erosion and deposition are also responsible for creating over 1,000 lakes in the BWCAW, which are interconnected by well-worn portage trails that link roughly 2,100 km of canoe routes (Heinselman, 1996).

With over 250,000 annual visitors, the BWCAW is the most popular Wilderness area in the United States, and many of those visitors come for the excellent fishing opportunities for walleye (*Sander vitreus*), northern pike (*Esox Lucius*), smallmouth bass (*Micropterus dolomieu*) and lake trout (*Salvelinus namaycush*) (USDA Forest Service 2012). There are no restrictions on the use of live bait in the BWCAW, and earthworms, along with leeches, are preferred over minnows by visiting anglers as they are easier to transport and keep alive without refrigeration and oxygenation over extended trips into the rugged and remote wilderness area (MN DNR 2019; personal experience). Both nightcrawlers and beavertails are readily available at bait shops, gas stations and canoe outfitters in wilderness gateway communities.

The number and distribution of visitors in the BWCAW is governed by a permit quota system from May through September. There are 55 designated entry points for overnight paddling trips into the wilderness and each entry point has a daily limit of permits that range from 1 to 27. Each permit allows for a traveling party of up to nine people and four canoes. The permit system is designed to spread visitor use and impact and help decrease competition for campsites. After entering, visitors are able to travel any route they choose and can exit the wilderness at any entry point, however, most visitors paddle looped routes back to their original entry point and parked vehicles. There are 2,063 designated campsites spread throughout the BWCAW and all are found along paddling routes adjacent to lakes or rivers. Camping is allowed at these designated

campsites only and campsite reservations are not allowed, meaning that campsite selections en route are not fully predetermined. No more than nine people can occupy a single campsite at one time.

While the vast majority of the BWCAW is non-motorized, there are several large lakes that lie partly in the BWCAW and allow the use of motors up to 25 horsepower. These motorized lakes are often popular entry points into the wilderness with large numbers of daily permits; private homes and cabins can be found along their shorelines outside the wilderness boundary.

Methods

Degree of earthworm invasion was assessed along 100 transects within the BWCAW during the summers of 2012 and 2013. A random sample of transect starting points was generated using ArcGIS (ESRI 2011) using all accessible lakeshores, campsites, and portage trails. This ensured adequate sampling across the entire wilderness to account for geographical differences in logging history, visitor use levels, proximity to population centers, and a west to east 2 degree C summer temperature and vegetation gradient. Lakeshore and campsite transects entered the forest at an azimuth perpendicular to the lakeshore. Portage trail transects entered the forest at an azimuth perpendicular to the selected point along the portage trail. A handheld GPS unit was used to navigate to lakeshore and portage trail transect starting points. Selected campsites were simply marked on our field maps. Transect lengths ranged from 20 m due to an impassable cliff, to ca. 500 m; the latter length was selected as the maximum given that 80% of land area within the BWCAW is within 500 m of a lakeshore (Rich 2005).

Degree of earthworm invasion was assessed at 10 m intervals along each transect using the Invasive Earthworm Rapid Assessment Tool (IERAT) (Loss et al. 2013). The IERAT is a five-stage earthworm invasion protocol that allows for rapid classification of invasion at a site based on distinct visual signatures left by different earthworm species due to their different feeding and burrowing habits including castings, middens, degree of litter fragmentation, and abundance of fine root presence in the O horizon. The IERAT protocol is particularly effective at identifying the onset of invasion by beaver tails and nightcrawlers, the species of greatest ecological concern in this region and the species most commonly used as fishing bait. Classification of a site can be completed in minutes, enabling researchers to efficiently cover geographically large areas of interest. As compared to methods used to extract earthworm from the soil, no heavy equipment or large quantities of water are required to be hauled in to sites, making data collection in remote, non-motorized areas more feasible. Data can be collected throughout the summer field season regardless of current soil moisture conditions, which can influence earthworm activity causing inaccurate results from extraction methods under dry conditions (Edwards, 1991). In addition to identifying the presence or absence of particular species at a site, IERAT rankings also provide an assessment of the associated level of ecological impact. All of these factors make the IERAT an ideal tool for a coarse-scale assessment of earthworm invasion in the expansive, remote and biodiverse forests of the BWCAW.

The IERAT stages largely correspond to the five sequential stages of earthworm invasion identified in this region by Holdsworth et al. (2007), with the number and types of earthworms as well as the ecological impact increasing with each stage. IERAT stage

1 is presumed to be earthworm free with a fully-intact forest floor. IERAT stage 2 is associated with the onset of invasion by small leaf worms (*D. octaedra)* that live exclusively in the litter layer, feeding on fungi and bacteria with limited impact to the forest floor (Holdsworth et al 2007). IERAT stage 3 is associated with the onset of invasion by beaver tails, *Aporrectodea* and *Octolasion spp.*, the removal of humus (O_a) layer and absence of fine plant roots. IERAT stage 4 is associated with the onset of invasion by nightcrawlers, the removal of leaf litter older than the previous autumn (O_i) and mineral soil (A-horizon) present. IERAT stage 5 is associated with the eventual dominance of nightcrawlers, complete removal of the forest floor (Oi, Oe, Oa) with only mineral soil (A-horizon) present at the surface (Figure 1).

Figure 1: This image taken along a portage trail near the BWCAW shows a stage five invasion with the forest floor completely removed, exposing the roots of a balsam fir. Photo credit: Doug Wallace

Field staff were trained in application of the IERAT by one of its authors prior to data collection (Loss et al. 2013). The IERAT dichotomous key was used in the field to assign an invasion stage ranking at a total of 2,518 points across 100 transects. Additional point and landscape predictor variables were obtained using geospatial data layers. Elevation, slope and compound topographic index (a proxy for soil moisture potential), were calculated for each point from a 10 m digital elevation model (DEM), resampled from a 1 m LiDAR-derived DEM of the region (https://gisdata.mn.gov). The presence or absence of logging at each point prior to wilderness designation was determined using maps of reconstructed fire history (Heinselman 1973). Campsite, portage trail and entry point locations, as well as entry point permit allocation data was obtained from the United States Forest Service (fs.usda.gov/superior, recreation.gov). Lakes, roads and a legislative boundary for the BWCAW were obtained from the State of Minnesota (gisdata.mn.gov). Distances from ranked points to physical features were calculated using ArcGIS (ESRI 2011) using Euclidean distance.

Table 1: Description of environmental variables assessed in association with degree of earthworm invasion in the BWCAW.

Variable	Units	Description
CSDist	m	Distance to nearest campsite
PortDist	m	Distance to nearest portage trail
LakeDist	m	Distance to nearest lakeshore
MLakeDist	m	Distance to nearest motorized lakeshore
RdDist	m	Distance to nearest road
Elev	m	Elevation
NumCS	#	Total number of campsites on nearest lake
NEPSea	#	Seasonal permit allocation of nearest entry point
Slp	%	Slope
CTI	#	Compound topographic index
Lat	degrees	Latitude
Lon	degrees	Longitude
Logged	P/A	Logging history

Statistical analyses were performed using R (R Development Core Team, 2018). Given the ordinal nature of our IERAT ranking response variable, a cumulative link mixed-effects model (CLMM) was used to assess the relationship between invasion stage and a suite of fixed effect predictor variables (Table 1) (Christensen, 2019). By using a CLMM versus a binned binomial approach, we hoped to elucidate rank-specific findings that might aid in a finer-scale understanding of invasion dynamics across different IERAT ranks and associated species assemblages. Transect number was included as a random effect in model fitting to control for non-independence among ranked points nested within transects (Harrison et al., 2018). To control for differences in scale and allow for predictive application of the model across the wilderness, continuous predictor variables were standardized by subtracting their population means and dividing by their population standard deviations prior to model fitting (Schielzeth 2010). Population

means and standard deviations for continuous landscape-related predictor variable were derived from a 30 m DEM of the region.

Model building followed an iterative process using the authors' domain knowledge and tests of statistical significance to guide final model selection. A full model using all single predictor variables was fit first. From there, several two-way interactions were tested for inclusion in the full model based on whether their inclusion resulted in significant reductions in Akaike's Information Criterion (AIC) at a p-value of 0.05. Fixed effect variables (excluding lower order interaction terms) were then tested for removal from the full model using a backward stepwise process until no further significant reductions in AIC were achieved.

Predictions of IERAT stages at observed points were then made using only the fixed effect coefficients from the final model. In evaluating the accuracy, sensitivity, and specificity of our final model we employed a binned threat-level approach used by Luiz et al. (2016). Specificity was defined as the combined percentage of correct classifications within rankings associated with no or little presumed ecological impact (IERAT stages 1-2). For example, a point observed as a 2, but predicted to be a 1, would be counted as a correct classification. Sensitivity was defined as the combined percentage of correct classifications within rankings associated with greater ecological impact (IERAT stages 3-5). Model accuracy was defined as the combined percentage of correct classifications across both low and high threat-level bins.

Our final model was then used to create a map of predicted stage of earthworm invasion across the entire BWCAW. Predictor variable values were derived from a 30m DEM of the study area. Elevation and slope were measured at the center of each 30m

pixel and all distance variables were measured using Euclidean distance from pixel center to the location of interest such as nearest campsite or portage trail. Standardized predictor variable values were input into the final model to generate a predicted IERAT stage for each 30m pixel. Finally, the percentage of land area in the BWCAW predicted to be in each invasion stage was calculated.

Results

Ninety-two percent of transects, the starting points of which were randomly selected to provide coverage across the accessible extent of the wilderness, contained points that showed signs of earthworm activity and were classified as stage 2 or greater (N = 100). All five IERAT stages of invasion were found across our 2,539 sampling points, indicating that multiple earthworm species assemblages, with varying degrees of ecological impact, are currently invading the BWCAW. Sixty-eight percent of sampled points were classified as stages 1 or 2, with no presumed or limited ecological impact, while 32% were classified in stages 3-5, with greater ecological impact due primarily to the presence of beaver tails and nightcrawlers (Figure 2).

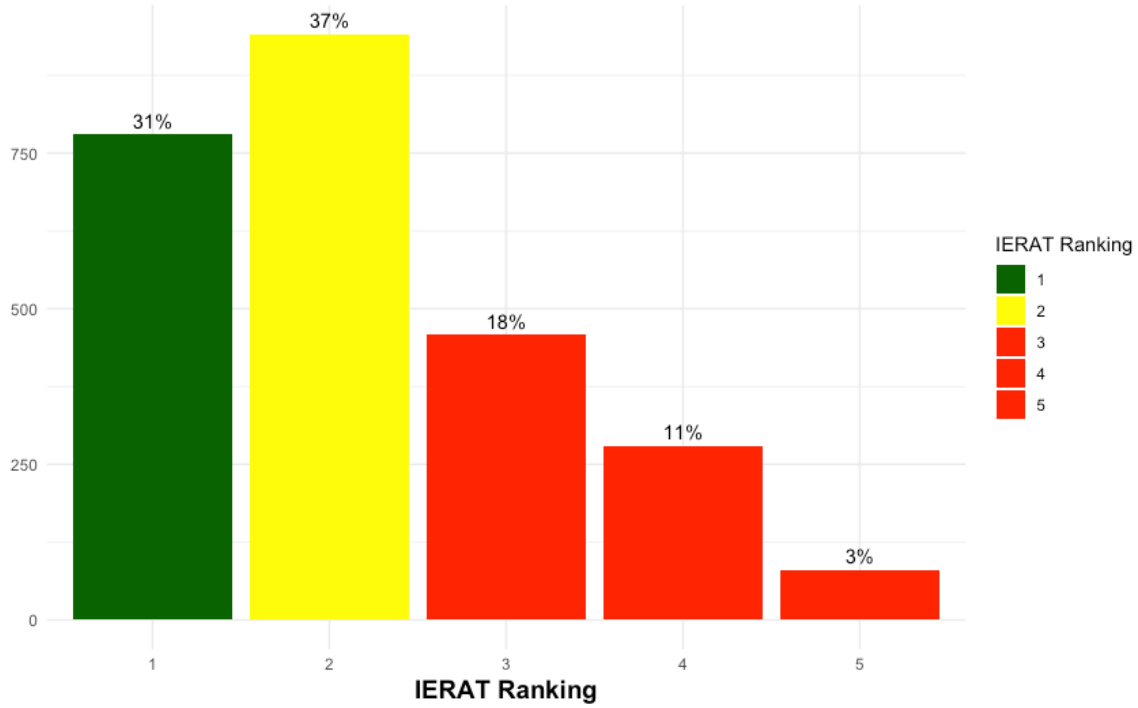


Figure 2: Frequency of observed IERAT rankings at sampled points in the BWCAW (n=2,539)

Table 2: Final CLMM fixed effect coefficients with IERAT ranking as the ordinal response variable. Significant interactions between Campsite Distance and Motor Lake Distance and Road Distance and Latitude are included. Coefficient values are expressed in standardized form.

Variable	Estimate	SE	z Value	P value
Campsite Distance	-5.4485	0.6134	-8.882	<0.0001
Portage Distance	-1.1462	0.3200	-3.582	0.0003
Lake Distance	0.7145	0.2796	2.555	0.0106
Motor Lake Distance	2.2517	0.5404	4.167	<0.0001
Road Distance	-0.2126	0.3259	-0.652	0.5142
Slope	-0.5427	0.1107	-4.902	<0.0001
Longitude	1.6976	0.3687	4.604	<0.0001
Latitude	-0.8898	0.4230	-2.103	0.0354
Elevation	-3.6828	0.4338	-8.489	<0.0001
Campsite Distance : Motor Lake Distance	1.6858	0.5481	3.076	0.0021
Road Distance : Latitude	-2.2533	0.4576	-4.925	<0.0001

As hypothesized, proximity to likely bait-dumping locations and several coarse measures of habitat suitability were found to be important predictors of earthworm invasion in the BWCAW. Campsite distance, portage distance and road distance were all negatively related to the probability of invasion at higher IERAT levels (Table 2). Campsite distance was the strongest predictor of both overall invasion probability (IERAT stages 2-5) and the probability of more advanced stages of invasion (IERAT stages 3-5) (Figures 3 and 4). We found a significant interaction between campsite distance and motor lake distance such that the effect of campsite distance on the probability of invasion at IERAT stages 3-5 increased as both campsite distance and motorized lake distance decreased (Figure 5).

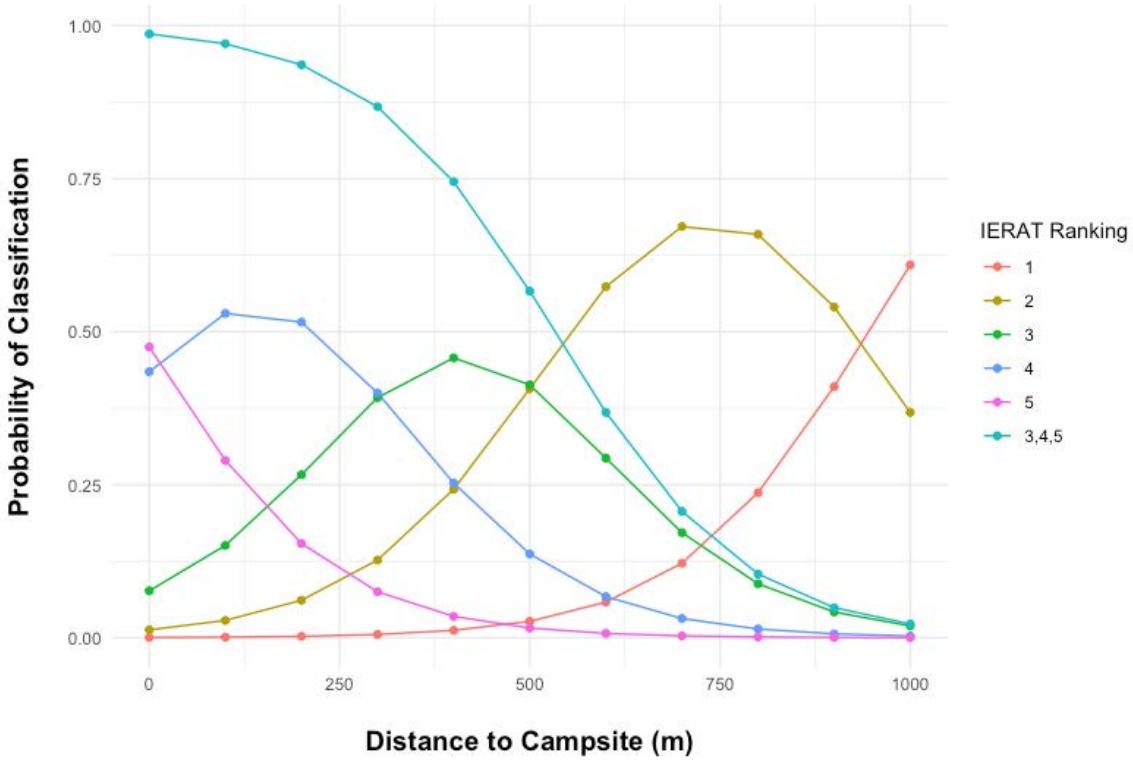


Figure 3: Probability of IERAT ranking as a function of campsite distance when motor lake distance was zero and all other model variables were held constant. Line 3,4,5 represents the cumulative probability of being classified in IERAT rankings 3-5.

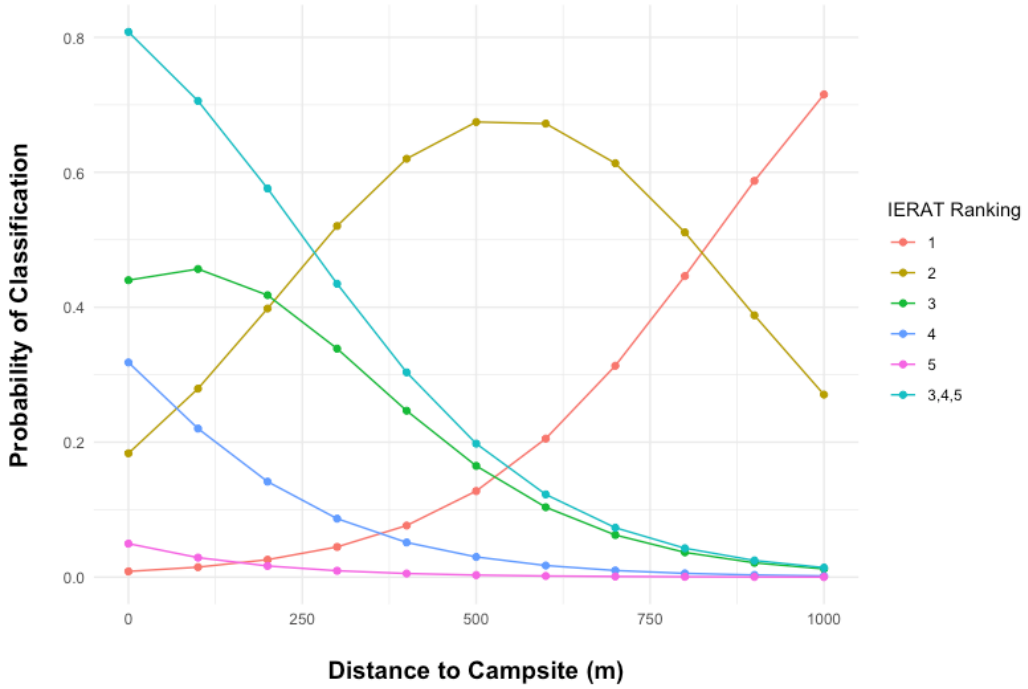


Figure 4: Probability of IERAT ranking as a function of campsite distance when motor lake distance was 10km and all other model variables were held constant. Line 3,4,5 represents the cumulative probability of being classified in IERAT rankings 3-5.

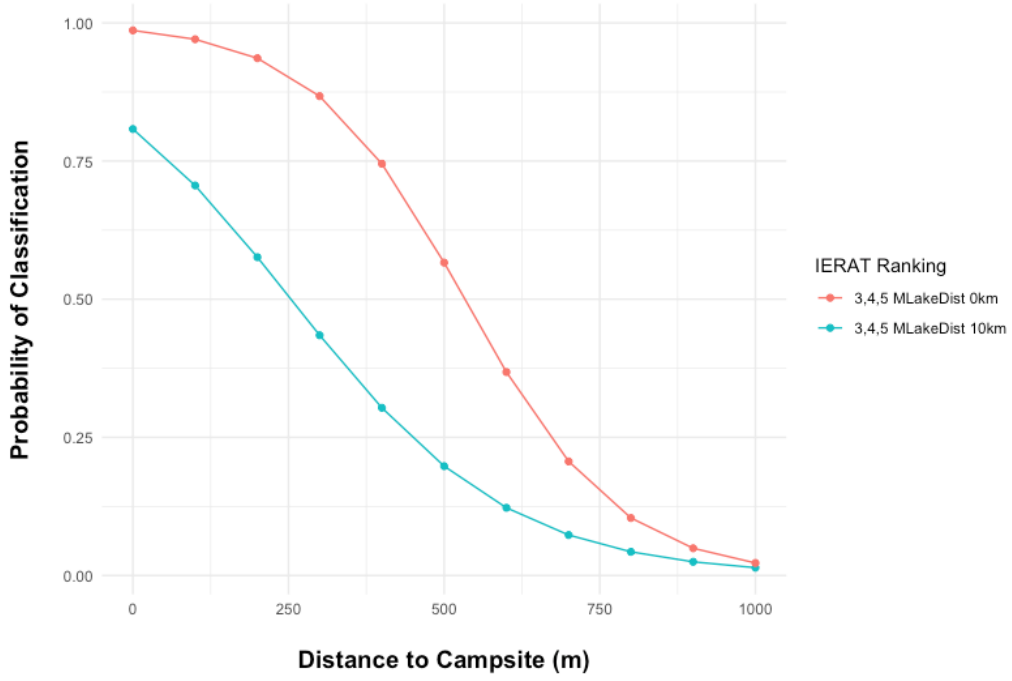


Figure 5: Cumulative probability of IERAT rankings 3-5 as a function of campsite distance when motor lake distance was set at 0km and 10km, and all other model variables were held constant.

Portage trail distance was found to be a significant predictor of invasion probability, although at a much lower magnitude than campsite distance (Table 2). We also found a significant interaction between road distance and latitude, such that the effect of road distance on the probability of invasion at higher levels was inverted across low and high latitudes (Figure 6). While road distance on its own was no longer significant after the inclusion of this interaction, it was retained in the final model as a supporting lower-order term (Table 2). Distance to the nearest lakeshore was moderately positively related to the probability of invasion at higher levels (Table 2). Total number of campsites on the nearest lake, seasonal permit allocation of the nearest entry point, and logging history were not found to be significant predictors of invasion.

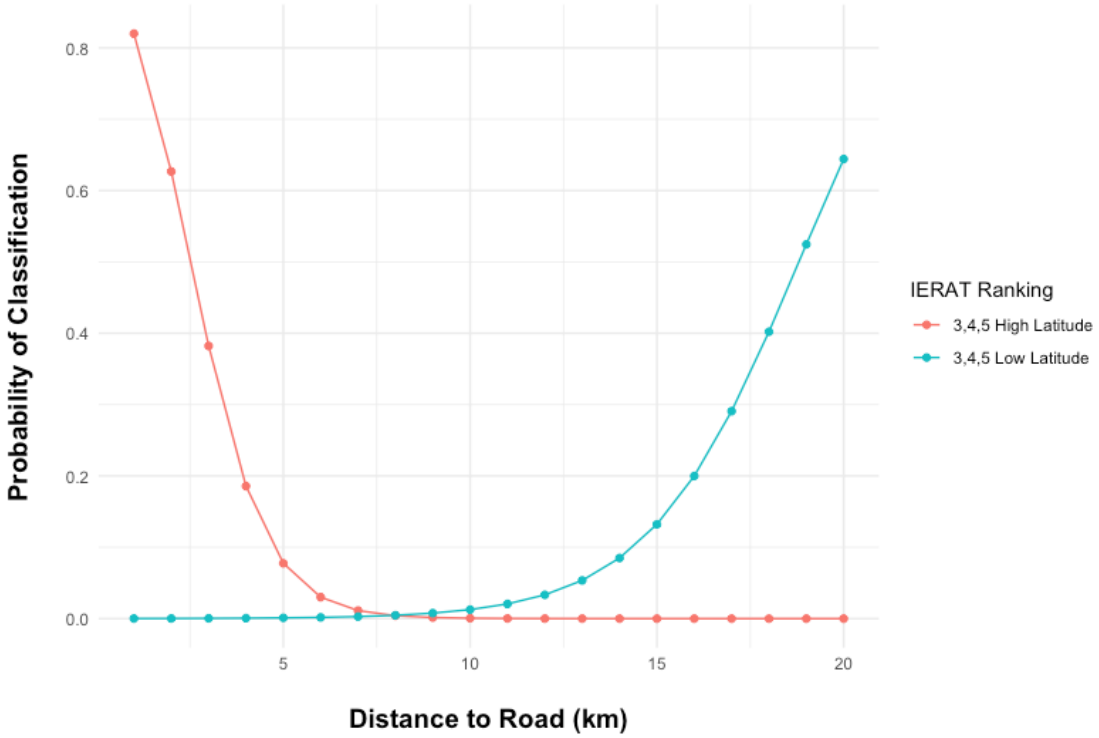


Figure 6: Cumulative probability of IERAT rankings 3-5 as a function of road distance at minimum and maximum latitudes, and all other model variables held constant.

Elevation and longitude were the strongest habitat suitability predictors of invasion probability (Figures 7 and 8). Elevation was negatively related to the probability of invasion at higher IERAT levels. Slope was also negatively related, but at a lower magnitude than elevation (Table 2). An increase in longitude (westerly movement), which was included as a coarse proxy for increased availability of both temperate and boreal deciduous leaf litter, was positively related to the probability of invasion at higher levels. Compound topographic index was not found to be a significant predictor of invasion.

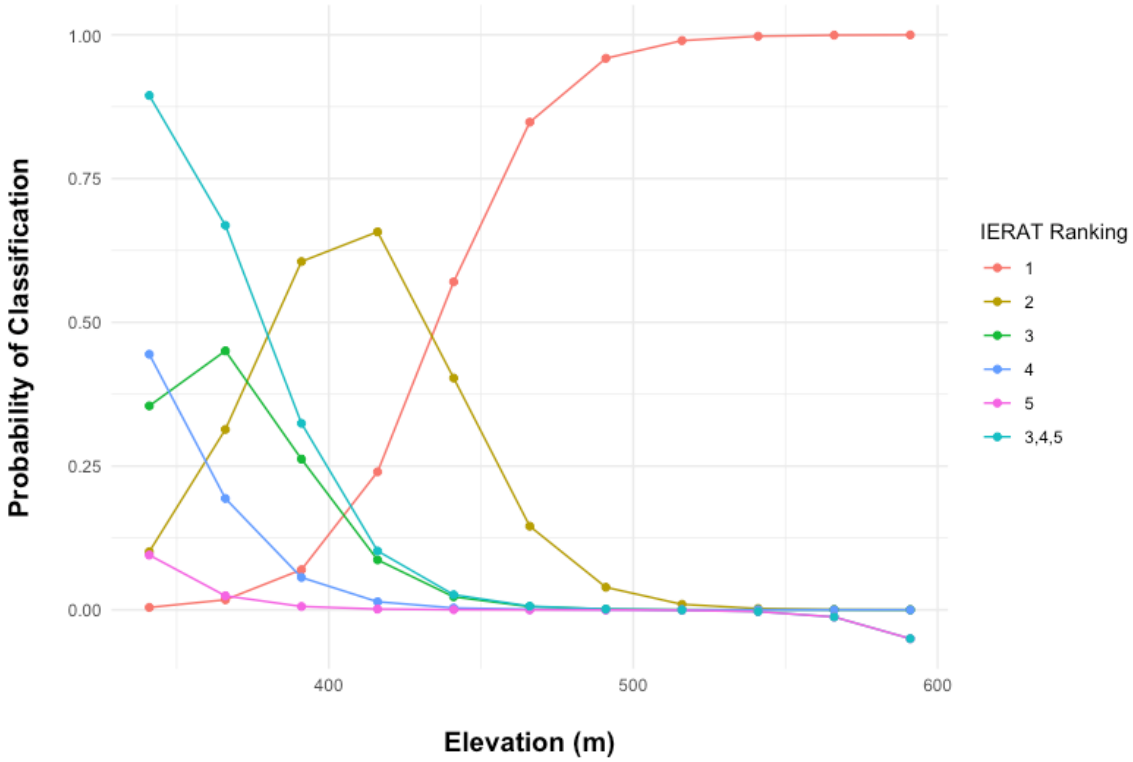


Figure 7: Probability of IERAT ranking as a function of elevation when all other model variables were held constant. Line 3,4,5 represents the cumulative probability of being classified in IERAT rankings 3-5.

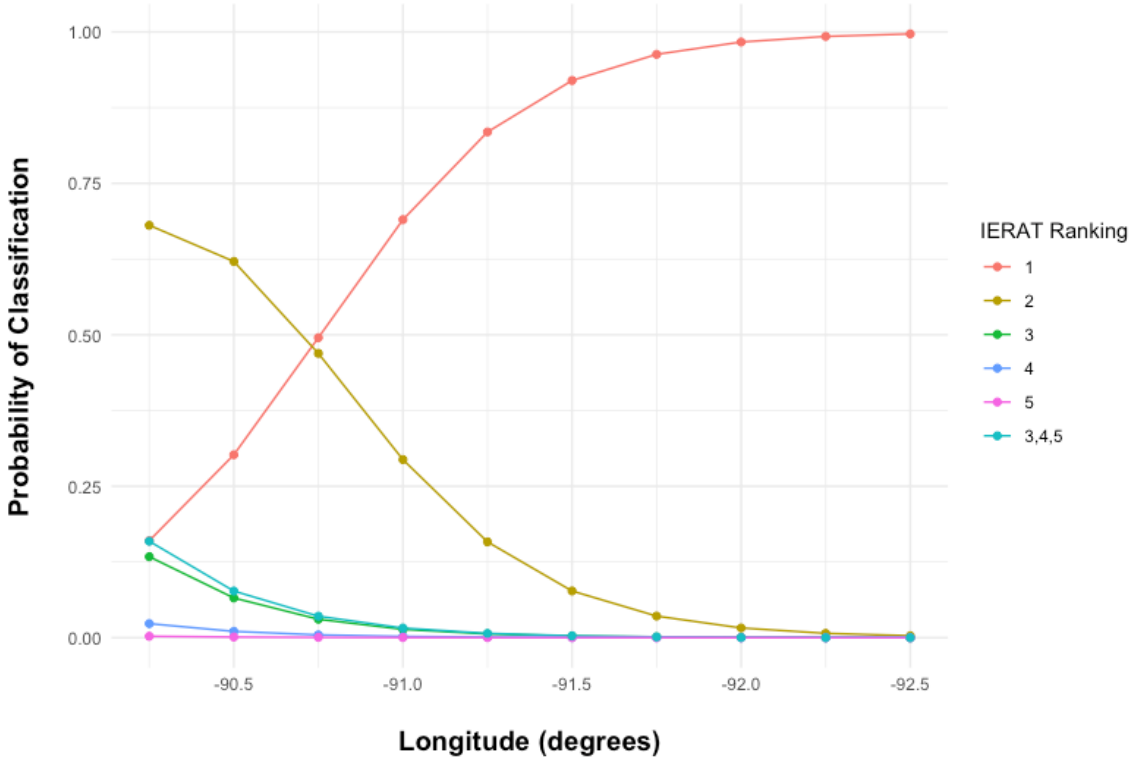


Figure 8: Probability of IERAT ranking as a function of longitude when all other model variables were held constant. The x-axis has been reversed to help visually convey a west to east gradient.

The accuracy, specificity and sensitivity of our final model were 0.72, 0.84, and 0.46 respectively. An invasion probability map of predicted IERAT stage across the entire BWCAW was created using our final model, resulting in a prediction that 33% of total land area in the BWCAW is currently invaded by earthworms (IERAT stages 2-5), and 10% is currently invaded by beaver tails and/or nightcrawlers (IERAT stages 3-5).

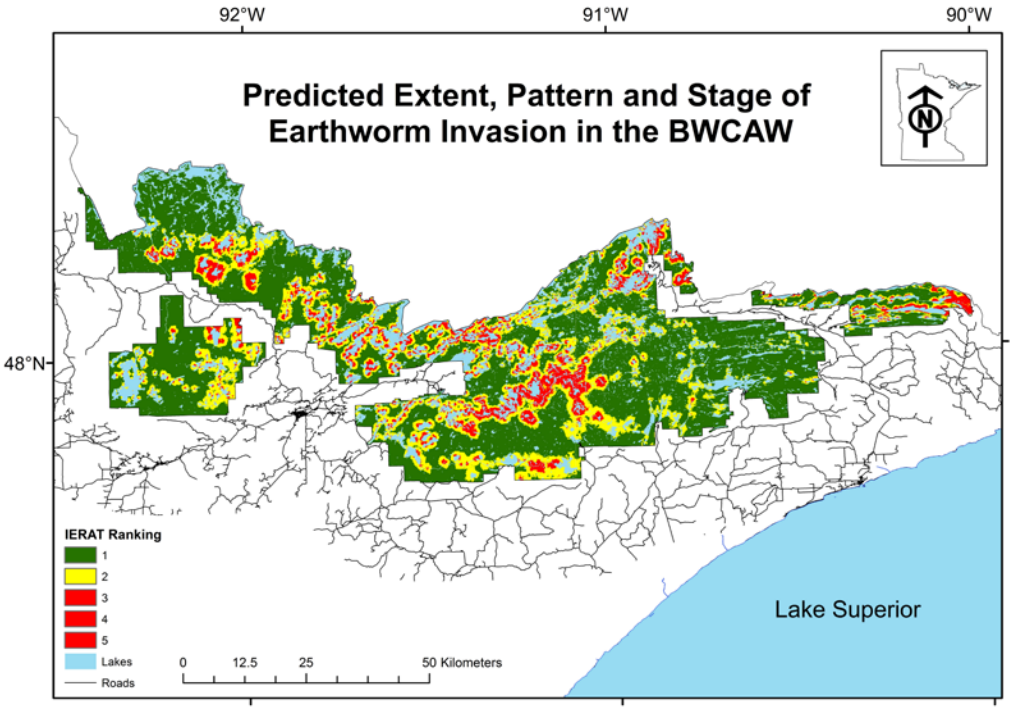


Figure 9: Map of predicted extent, pattern and stage of earthworm invasion in the BWCAW.

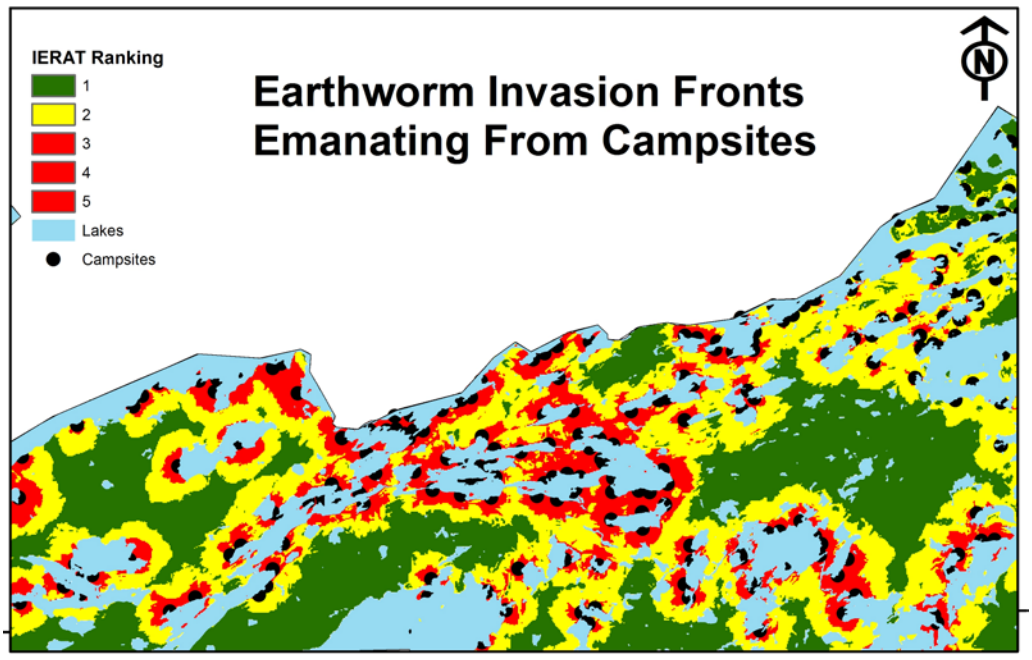


Figure 10: Map illustrating the dominant spatial pattern of earthworm invasion in the BWCAW, with invasion fronts emanating from campsites, which are the most likely bait-dumping sites in the wilderness. IERAT rankings 3, 4, and 5 were mapped with the same color, collectively indicating advanced earthworm invasion.

Discussion

Results from this coarse-scale survey indicate that earthworm invasion in the BWCAW is widespread, yet incomplete, with campsites serving as the primary epicenters of invasion. Modeling results indicate that the spatial pattern of earthworm invasion in the BWCAW is driven primarily by anglers dumping their unused earthworm fishing bait at campsites. The probability of invasion by beaver tails and/or nightcrawlers at campsites on motorized lakes, and at campsites 10km away from motorized lakes, is 0.99 and 0.81 respectively. As the distance away from those campsite increases, the probability of invasion by beaver tails and/or nightcrawlers, the two species most commonly sold as fishing bait in this region, drops precipitously (Figures 3 and 4). The significant interaction between campsite distance and motor lake distance indicates that campsites on or near motorized lakes are somewhat more likely to be invaded. The handful of motorized lakes found on the outer edges of the wilderness such as Lac La Croix, Basswood, Seagull and Saganaga are popular fishing lakes known for healthy populations of all four primary game fish species in this region. In fact, the Minnesota state record walleye was caught in the Seagull river at Saganaga lake. A reputation for good fishing combined with easy access for overnight paddlers, day-trippers, and local anglers alike increases fishing pressure on these lakes, in turn increasing the chances that bait dumping at campsites found along their shores has occurred at some point in time. However, regardless of how deep one travels into the wilderness, bait-dumping at campsites appears to be the primary mechanism of both introduction and spread of invasive earthworms in the BWCAW.

To further illustrate that point, we found an interesting curvilinear relationship between campsite distance and the probability of invasion by *D. octaedra.* While *D. octaedra* is not a species typically used as fishing bait, it can be found mixed in with beaver tails and nightcrawlers in retail containers marketed as containing the larger species (Tiunov et al., 2006; Hale 2008). As campsite distance increased to 700 m, the probability of IERAT stage 2 (initial invasion by *D. octaedra*) increased to a peak of 0.67, before it began to fall with further increases in campsite distance in relation to presumed earthworm free conditions (IERAT ranking 1) (Figure 2). Studies have shown that *D. octaedra* is able to spread via natural diffusion at a faster per year rate than both beaver tails and nightcrawlers as it lives solely in the litter layer, making it more of a habitat generalist, and it is parthenogenetic (Holdsworth et al 2007). As such, *D. octaedra* is often found beyond the leading edge of an invasion by beaver tails and nightcrawlers, with their abundance declining at the leading edge as the littler layer is eliminated (Hale et al 2005). Our results are consistent with this phenomenon, indicating that bait dumping is also a significant introduction mechanism for *D. octaedra* in the BWCAW via "contaminated bait", and suggesting that the distance of *D. octaedra* invasion fronts from campsites could possibly help estimate the timeframe of the initial introduction of beaver tails and nightcrawlers, along with predictions of their future spread.

While campsites appear to be the most likely bait-dumping sites in the BWCAW, distance from portage trails was a significant predictor of invasion probability (Table 2). In addition to campsites, portage trails are the other primary locations where visitors to the BWCAW spend any significant time on land, and our results indicate that they are

also serving as bait-dumping sites. Carrying live bait on a wilderness canoe trip can be messy and odious work (D. Chaffin personal experience). Anglers may be choosing to discard their bait en route to avoid carrying it across portage trails, which can be rugged and up to 2 km in length. These results are consistent with other studies that have found strong spatial correlations between earthworm invasion probability and proximity to sites where the dumping of earthworms used as fishing bait is more likely, including boat landings and cabins (Holdsworth et al., 2007, Cameron and Bayne, 2007).

Figure 11: A discarded container of earthworm fishing bait found along a BWCAW portage trail while conducting fieldwork for this study. Photo credit: D. Chaffin

Roads are known to be effective corridors for the spread of invasive species, and proximity to roads has been found to be a significant predictor of earthworm invasion in many other studies (Paudel et al., 2016; Saltmarsh et al., 2016; Shartell et al., 2013;

Cameron and Bayne, 2009; Cameron and Bayne, 2007; Holdsworth et al., 2007). Results from our study indicate that the impact of proximity to roads on invasion probability in the BWCAW is inversely related to latitude. At high latitudes the probability of invasion at higher stages decreased with increasing road distance, while at low latitudes the probability of invasion increased with increasing road distance (Figure 6). Most roads along the most southerly border of the BWCAW are less used, unpaved forest service roads. These roads were used for logging in the BWCAW prior to Wilderness designation, and continue to be used for present-day logging outside the Wilderness border. However, most logging in this area occurs in the winter months, which could limit its role in earthworm dispersal and explain why logging history was not found to be a significant predictor of invasion. More heavily used, paved roads such as the Gunflint Trail emanating from the town of Grand Marais, MN in the east and the Fernberg and Echo Trails emanating from the town of Ely, MN in the west, are generally found at higher latitudes and are associated with greater numbers of people, homes, cabins and resorts. We suspect that at higher latitudes, it is actually proximity to these more developed areas with proven bait-dumping sites such as cabins and fishing resorts that is driving the increase in invasion probability. And along the far southern border of the BWCAW, the increase in invasion probability with increasing road distance is most likely due to the increased proximity to campsites and portage trails as one moves north into the wilderness. However, the roadless nature of the Wilderness and the pace at which earthworms may be spreading into the BWCAW from introductions associated with roads outside its border make it less of an overall factor currently than proximity to campsites.

Distance from the nearest lakeshore was positively related to the probability of invasion at higher IERAT stages, albeit moderately (Table 2). This positive relationship may be due to the fact that as distance from a lakeshore increases, chances of getting closer to a campsite on another lake or a portage trail, and intersecting with the invasion fronts emanating from those sites increases. Or perhaps, as distance from rocky lakeshores in the BWCAW increases, soil depths more conducive to the epi-endogeic beaver tail and anecic nightcrawler also increase.

In addition to the distanced-based predictor variables, modeling results indicate that several environmental variables are exerting physical and biological controls over the probability of earthworm invasion in the BWCAW. Next to campsite distance, elevation was the second strongest predictor variable with the probability of invasion at higher ranks decreasing to just 0.01 at 466 (m), which is just below the mean elevation of 469 (m) of our dataset (Figure 7). Slope also had a negative relationship with invasion probability, but at a much lower magnitude than elevation (Table 2). While it is difficult to account for the multiple ways that these two variables may be influencing earthworm invasion in the BWCAW, it would appear that overall accessibility by both humans and worms plays a role. Steeper slopes and higher elevations can pose a physical barrier to earthworms in expanding their range from initial introduction sites. In the BWCAW, steeper and higher elevation sites are also more likely to have thinner soils or exposed bedrock not conducive to establishment by epi-endogeic and anecic species such as beaver tails and nightcrawlers. All campsites in the BWCAW, where modeling indicates that bait dumping is most likely, are found adjacent to lakeshores at flatter and lower elevation sites relative to their immediate surroundings.

Proportion of overstory tree species with leaf litter that is preferred by earthworms has been shown to be a strong predictor of earthworm abundance (Fisichelli et al 2013; Shartell et al 2013). Due to a west to east 2 degree C summer temperature and vegetation gradient across the BWCAW, there is a higher abundance of temperate deciduous species preferred by earthworms over boreal conifer species, in the western region of the wilderness. A recent survey of temperate tree species in the BWCAW found 1,405% greater abundance of red maple trees >15 cm d.b.h in the western third of the wilderness compared to the eastern third (author unpublished data). As such, the longitude of sampled points was used in model building as a coarse proxy for proportion of preferred overstory species. Results show a clear increase in probability of invasion by beaver tail and nightcrawlers as one moves from east to west in the BWCAW, which could support our hypothesis that broad landscape-level patterns of forest composition may be influencing establishment success and spread of earthworms in the BWCAW (Figure 9). However, caution should be exercised in interpreting the role of longitude given the extremely coarse nature of the association with preferred overstory species as well as the potential for other geographic driven factors such as varying visitor use levels, campsite density, or proportion of accessible land area.

Our prediction that 33% of total land area in the BWCAW is currently invaded by earthworms (IERAT stages 2-5), and 10% is currently invaded by beaver tails and/or nightcrawlers (IERAT stages 3-5), is significantly higher than an estimate of invasion extent in the boreal forests of Alberta (i.e., 9% invaded by *D. octaedra*, corresponding to IERAT stage 2) where more recent and lower levels of human use, as well as similar forest types, make it a point of comparison for the BWCAW (Cameron et al., 2009).

While the BWCAW is a remote boreal wilderness with a significant proportion of its land area inaccessible to the typical visitor, several unique characteristics appear to be driving invasion extent and stage beyond what has been documented in other similar study areas. As America's most popular wilderness area, the BWCAW hosts over 250,000 visitors per year, many of them anglers who carry in live bait. To accommodate all of those visitors, 2,063 campsites are spread throughout the wilderness and a permit system helps spread visitor use at these campsites across the landscape. Research has shown that human-mediated "jump dispersal" of earthworms via the dumping of fishing bait at new introduction sites is a more important driver of aerial invasion expansion than the natural spread of current invasion fronts (Cameron et al., 2008). While the wide geographic distribution of visitor use in the BWCAW is intended to reduce overall human impact on the wilderness ecosystem, it seems to be having a perverse effect in providing a highly effective, human-facilitated distribution system for invasive earthworms.

Estimates of invasion extent in Minnesota and the surrounding Western Great Lakes region are significantly higher than what our study found in the BWCAW. Holdsworth et al. (2007), estimated that 82% of hardwood stands in Wisconsin's Chequamegon National Forest are invaded by an assemblage of species that includes beaver tails and nightcrawlers. A lack of necessary spatial data layers prevented a corresponding estimate for Minnesota's Chippewa National Forest, which lies approximately 150 miles southwest of the BWCAW, but plot level data of earthworm abundance was similar between the two National Forests indicating a similar trend. Similarly, Shartell et al., estimated that 41% of their study area in the upper peninsula of Michigan is currently invaded by nightcrawlers. Given that the BWCAW has been a popular fishing

destination for several decades and all earthworm species present are able to overwinter at its more northerly latitude, we suspect that a higher proportion of conifer leaf litter less preferred by earthworms plays a key role in our lower estimates of invasion as compared to other maple dominated sites in the Western Great Lakes region. However, it should be noted that predictions from our final model against observed IERAT rankings of 3, 4 and 5 from our sample dataset exhibited a high proportion of false negatives, meaning those points were predicted to be at a lower invasion stage than observed. The proportion of false negative predictions for IERAT stages 3, 4 and 5 against observations was 55%, 79% and 100% respectively. Conversely, the proportion of false positive predictions across all IERAT stages was 7% (IERAT stage 1), 23% (IERAT stage 2), 18% (IERAT stage 3), 0% (IERAT stage 4) and 0% (IERAT stage 5). These results indicate that our predictions that 33% and 10% of total land area in the BWCAW is currently invaded by earthworms (IERAT stages 2-5) and beaver tails/nightcrawlers (IERAT stages 3-5) respectively is conservative, and actual invasion extent and stage are likely higher. Future research on the extent and stage of earthworm invasion in the BWCAW would benefit from a finer-scale understanding of the role that forest composition may play in inhibiting or enabling the colonization and spread of beaver tails and nightcrawlers and the probability of later IERAT stages of invasion.

Conclusions

Sixty-nine species of greatest conservation need are known or predicted to occur within Minnesota's Border Lakes ecological subsection, much of which falls within the BWCAW (MN DNR, 2006). As the near-boreal forests of the BWCAW are close to their southern range limit, this appears to make certain of its species including balsam fir,

black spruce, white spruce and jack pine particularly sensitive to climate change (Fisichelli et al 2013, Reich et al 2015). Given that sensitivity, and the additional sensitivity of these forests to indirect effects of climate warming on soil moisture plus the compounding effects of earthworm invasion, namely warmer and drier soils, collectively this suggests a high potential for strong interactive negative effects on the boreal conifers (Reich et al 2018). While our results confirm that earthworm invasion fronts are well-established across the entire BWCAW, due primarily to the dumping of earthworms at campsites by anglers, the majority of the wilderness likely remains free of the more ecologically damaging species, including beaver tails and nightcrawlers. The semi-random process of campsite selection by visitors and the stochastic nature of earthworm dumping by anglers make it unlikely that earthworms have already been introduced at all 2,063 campsites. The sheer size and intactness of the BWCAW, combined with its higher proportion of conifer species, seems to be acting as a present-day buffer to the spread of invasion fronts from both outside and inside the wilderness. While human-facilitated introduction of earthworms at new sites in the BWCAW appears to be the primary driver of aerial invasion expansion, a predicted increase in abundance of deciduous tree species that produce leaf litter more preferred by earthworms could also facilitate greater natural diffusion of existing invasion fronts in the coming decades. Large areas within the BWCAW have recently been subject to compound disturbance (blown down followed by wildfire), which leads to changes in the dominant tree species from spruce, fir and pine to birch and aspen. Species such as American basswood (*Tilia Americana*) and red maple are also predicted to increase in abundance within the BWCAW under climate change, as are compound disturbance events (Johnstone et al.

2016; Frelich and Reich, 2009). We conclude that management interventions focused on preventing new introductions at currently un-invaded sites, and repeated introductions at currently invaded sites is the only available and effective strategy for slowing the spread of invasive earthworms in the BWCAW today and in the future. Such interventions could include an increase in education efforts with BWCAW anglers about the effects of invasive earthworms and the illegality of dumping live bait, or restricting the use of live-bait in the BWCAW, as was implemented in the adjoining Quetico Provincial Park in 2007. (https://www.ontarioparks.com/park/quetico/camping).

Temperate Tree Seed Source Abundance and Spatial Distribution in the Boundary Waters Canoe Area Wilderness (U.S.A)

Introduction

Climate change is projected to cause a redistribution of tree species habitats across northern Minnesota by the end of the century (Duveneck et al., 2014; Frelich and Reich, 2009; Galatowitsch et al., 2009). This presents a complex and unplanned for variable in contemporary management of the forests of the Boundary Waters Canoe Area Wilderness (BWCAW), a 400,000 ha federal wilderness area in northeastern Minnesota. Regional climate change projections of increased temperatures, stable to decreasing precipitation, and a resulting decrease in precipitation-to-evaporation ratios are expected to cause the prairie-forest and boreal-temperate forest ecotones in northern Minnesota to shift to the northeast, as they have during past episodes of warming (Frelich and Reich, 2009; Davis and Shaw, 2001). Shifts in suitable tree species habitat of 100 km to 500 km per century are predicted to occur, far exceeding estimates of historical tree species range shifts in the region of 20 km to 40 km per century during the mid-Holocene warm period (Galatowitsch et al., 2009; Davis and Shaw, 2001).

The BWCAW is located in a mid-continental, moderately high latitude region where the magnitude and velocity of climate change is predicted to be more than the global mean (Loarie et al, 2009; Frelich and Reich, 2009; Christensen et al., 2007;). Its western border is within 250 km of the prairie-forest ecotone, while the boreal-temperate forest ecotone runs through the wilderness. Although not fully boreal, forests in the BWCAW are nevertheless dominated by boreal species at or near their southern range limits, making some of its species particularly sensitive to climate change (Fisichelli et al

2013, Reich et al 2015). These and other factors have led to projections of boreal forest community decline in northeastern Minnesota, and potential extirpation of the boreal biome from the BWCAW and Minnesota altogether by the end of the century (Swanston et al., 2018; Ravenscroft et al., 2010; Galatowitsch et al., 2009). These factors also raise questions about whether a successful transition from boreal to temperate forest will occur given the disparity between estimates of historical tree migration rates, and the rate at which northern temperate tree species may need to migrate in the future to keep pace with a rapidly changing climate (Frelich and Reich, 2009; Galatowitsch et al., 2009; Walker et al., 2002).

Numerous studies have modeled potential future climate change induced tree species range shifts in northern Minnesota, and within the BWCAW specifically, to support climate change adaptation planning efforts (Swanston et al., 2018; Duveneck et al., 2014; Ravenscroft et al., 2010; Xu et al., 2010; Galatowitsch et al., 2009; Iverson and Prasad, 2007; Walker et al., 2002). There are two broad classes of these predictive models: species distribution models (SDMs) and process models. SDMs look at the current distribution of tree species against a set of environmental variables, like climate, and then predict changes in distributions based on changes in future climate and suitable habitat as defined by current distributions. SDMs are largely founded in ecological niche theory (Pearson and Dawson, 2003). Process models do not assume that current distributions are in equilibrium with current climate, and they incorporate species-specific physiological processes, such as dispersal ability, in predicting future distributions under climate change (Iverson and McKenzie, 2013; Morin et al., 2008; Pearson and Dawson, 2003).

The Climate Change Tree Atlas (CCTA), a product of the U.S. Forest Service's Northern Research Station, is a robust SDM that models current and predicted distributions of 134 eastern U.S. tree species across the Eastern United States under climate change (Iverson et al., 2007). LANDIS-II is a process model that simulates landscape level changes in forest composition resulting from the interaction of a suite of user-defined processes such as climate change, disturbance, harvest levels and seed dispersal (Scheller et al., 2007). As part of a recent assessment of Minnesota forest ecosystem vulnerability to climate change, both models were applied to similar portions of the Laurentian mixed forest in northeastern Minnesota, which includes the BWCAW, under both low and high emissions scenarios (Handler et al., 2014). Results showed strong agreement between models in projecting declines in suitable habitat (i.e., CCTA) and relative abundance (i.e., LANDIS-II) of black spruce (*Picea mariana)*, balsam fir (*Abies balsamea)*, quaking aspen (*Populus tremuloides)*, paper birch (*Betula papyrifera)*, and jack pine *(Pinus banksiana*, high emissions scenario only), with these species likely being lost from the landscape under a future high emissions scenario. Model results also showed strong agreement in projecting increases in suitable habitat (i.e., CCTA) and relative abundance (i.e., LANDIS-II) for seven of nine northern temperate deciduous tree species currently believed to be at low abundances in the BWCAW: American basswood (*Tilia americana*), northern red oak (*Quercus rubra*, declines under high emissions), bur oak (*Quercus macrocarpa*), green ash (*Fraxinus pennsylvannica*), American elm (*Ulmus americana*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*, declines under high emissions). The CCTA also projected large increases in suitable habitat for northern pin oak (*Quercus ellipsoidalis*) and silver maple (*Acer saccharinum*).

Dispersal ability has been shown to be an important process to account for in predicting potential future distributions of tree species under climate change (McLachlan et al., 2005; Levin et al., 2003). Using the LANDIS-II model to predict future tree species composition in the BWCAW under climate change, researchers found colonization (partly a function of dispersal ability) to be the dominant process determining forest succession in the BWCAW over time periods greater than 100 years or under a disturbance regime consisting of more frequent fires (Xu et al., 2012). Similarly, in applying the PHENOFIT process model to predict future distributions of 16 North American tree species under climate change (including three species projected to increase in abundance in the BWCAW: silver maple, bur oak and American elm) researchers found that colonization of new habitat at northern range boundaries for most study tree species was primarily limited by dispersal ability (Morin et al., 2008).

Tree species range shifts are related to colonization success, which is related to species-specific dispersal characteristics and the abundance and spatial distribution of seed-bearing trees on the landscape. The CCTA and LANDIS-II models both incorporate aspects of species-specific dispersal abilities in modeling projections of future tree species range shifts (Matthews et al., 2011). However, their respective baselines of current abundance and spatial distribution of seed-bearing trees from which modeled dispersal events emanate are based on data sources that may not provide accurate estimates of temperate tree seed sources at a fine enough resolution to inform landscape level management decisions (Swanston et al., 2018). The CCTA utilizes tree data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program, which has a resolution of approximately one survey plot for every 6,000 acres of forestland, or 25 km^2

(Iverson and Prasad, 2007). FIA data has been previously unavailable within the BWCAW, however plots were added to the wilderness as part of an FIA intensification project in 2001 to assess the impacts of a large-scale blowdown event, with data now available from the 2011-2015 Minnesota state survey. LANDIS-II uses a combination of a satellite-derived vegetation classification of canopy dominant species with stage age and forest community type maps from the 1970s to assign each pixel an initial forest composition type and age class at a resolution of 28.5 m x 28.5 m (Scheller et al., 2007). While the LANDIS-II resolution is much finer than the CCTA, the satellite –derived vegetation classification based on canopy dominants likely misses low abundance non-boreal species in the canopy as well as non-boreal species in the understory that may be of seed-bearing age. Whether due to coarse-resolution or limitations in satellite imagery technique, imprecise estimates of northern temperate tree seed sources could lead to over and/or under estimates of the likelihood of successful colonization of the BWCAW by temperate tree species under climate change, making adaptive management decisions more difficult. Given the unprecedented velocity of projected future climate change in the region, the comparatively slow pace of historical tree migrations during previous episodes of climate warming, and the significant ecological, cultural and recreational value of the BWCAW, it is important that future management decisions be informed by landscape-level data where possible. To our knowledge, the FIA and satellite-derived datasets employed by the CCTA and LANDIS-II models are the only available projections of future forest composition in the BWCAW.

The purpose of this study was to improve our understanding of whether the forests of the BWCAW are poised to successfully transition to temperate forest types as

boreal tree species decline under climate change. To do so, we assessed the abundance and spatial distribution of northern temperate tree species currently at low abundances in the BWCAW, but whose populations are expected to increase to varying degrees under different climate change scenarios, at a finer resolution than currently available. We hypothesized that: 1) red maple and northern red oak would be the most abundant northern temperate species in the BWCAW, 2) our abundance estimates for all northern temperate tree species in the BWCAW would be higher than comparable FIA-derived estimates, and 3) the spatial distribution of northern temperate tree species in the BWCAW would closely follow the existing west to east summer temperate gradient, with greater abundances in the west and less in the east.

Methods

Study area

The BWCAW is a federal, paddle-only Wilderness area located within the Superior National Forest in far northeastern Minnesota, USA. Spanning 400,000 ha of forest, it contains over 1,000 lakes interconnected by hundreds of miles of portages and streams that link approximately 1,300 miles of canoe routes (Heinselman, 1996). There are 55 designated entry points for overnight paddling trips and over 2,000 designated campsites, all of which are found along established paddling routes adjacent to lakes or rivers. Given its roadless and non-motorized nature, fieldwork locations in this large and remote wilderness area are largely limited to areas that are accessible by canoe or on foot.

The entire BWCAW is underlain by Pre-Cambrian rock, primarily granite but also gabbro, greenstone and some slates. Its soils are the result of sandy and gravelly loam

glacial deposits, and soils are generally thin with rocky outcroppings and exposed bedrock common along lakeshores and on ridge tops (Ohmann & Ream, 1971).

The BWCAW's forests have been described as "near boreal," and are dominated by boreal tree species near their southern range limits, which appears to make certain of its species including balsam fir, black spruce, white spruce (*Picea glauca*) and jack pine particularly sensitive to climate change (Fisichelli et al 2013, Reich et al 2015). Historically, fires of varying intensity and frequency created a patchwork of pure and mixed stands of boreal species including jack pine, black spruce, balsam fir, quaking aspen, and paper birch. Red pine (*Pinus resinosa)* and eastern white pine (*Pinus strobus)* stands are often found on leeward lakeshores and islands where fire intensity was typically less, and stands of northern white cedar (*Thuja occidentalis)* are often found on wet sites (Frelich & Reich, 1995; Heinselman, 1996). While logging is currently prohibited in the BWCAW, approximately 50% of the area within its current borders was logged between the 1890s and the late 1970s, serving as a primary form of disturbance during those years (Heinselman, 1996).

Some northern temperate species are also present in the Wilderness, primarily red maple and northern red oak, with some stands found on the western side where summer temperatures are on average 2°C warmer (Ohmann & Ream, 1971; Heinselman, 1996; author unpublished data). To account for this existing west to east temperature and vegetation gradient in our survey, we divided the BWCAW into three study regions of approximately equal area using north-south county line boundaries.

Study species

Our study focused on northern temperate tree species currently at low abundances in the BWCAW, but whose populations are expected to increase to varying degrees under different climate change scenarios. These species as defined in Frelich and Reich (2009) include: American basswood, northern red oak, bur oak, northern pin oak, green ash, American elm, red maple, silver maple, and yellow birch.

Line transect distance sampling

Line transect distance sampling is a well-established and widely used method of estimating the abundance of biological populations (Thomas et al., 2010). As its name implies, abundance estimates are derived from distance measurements from a line to an object of interest (Buckland et al., 2000). As one advances along a line transect, perpendicular distance measurements from the line to a visual detection of the object of interest are recorded, recognizing that not all occurrences will be successfully detected. The distribution of recorded distance measurements are then used to estimate the proportion of the object of interest that was visually detected within the transect strip area defined as $2wL$, where w is the maximum visual observation distance and L is total transect length. To avoid models being overly influenced by limited long-distance observations, w is often truncated to a constrained maximum distance (Thomas et al., 2010). With an estimate of the proportion visually detected within the surveyed area, we can then estimate abundance for both the surveyed area and the larger study area of interest (Thomas et al., 2010).

Three key assumptions underpin line transect distance sampling. First, all objects of interest directly on the transect line are detected with certainty, meaning at a distance

of 0 the detection probability is 1. Second, objects of interest do not move while distance measurements are being taken, which could undermine the third key assumption, which is that perpendicular distance measurements from the transect line are exact (Thomas et al., 2010)

While line transect distance sampling has a long history of use in the assessment of wildlife populations, its use in plant surveys has been a more recent development (Buckland et al., 2007). Laser rangefinders combined with the stationary nature of plants makes it relatively easy to obtain precise distance measurements in the field. And in cases where the plant species of interest is at low abundance and is visually distinct from surrounding vegetation, line transect distance sampling has been shown to be an efficient way to generate robust abundance estimates across large geographic areas when compared to more traditional plot survey approaches (Kissa & Sheil, 2012). For these reasons we employed line transect distance sampling in our survey of northern temperate tree species currently at low abundances within the geographically expansive and remote BWCAW. While the number of temperate tree species surveyed was fairly high (10), currently low abundances and distinct visual differences in leaf and bark morphology compared to the boreal tree species that currently dominate the landscape made quick and accurate visual identification in the field possible.

Survey procedure

Line transect distance sampling was employed along 100 transects within the BWCAW during the summers of 2012 and 2013 (Figure 12). St. Louis, Lake and Cook county lines were used to divide the BWCAW into three regions (i.e., west, central, and east) of approximately equal area and a stratified random sample of transect starting

points was generated using ArcGIS (ESRI 2011) using all accessible lakeshores, campsites and portage trails. This ensured adequate sampling across the entire wilderness to account for the west to east summer temperature and vegetation gradient. Lakeshore and campsite transects entered the forest at an azimuth perpendicular to the lakeshore. Portage trail transects entered the forest at an azimuth perpendicular to the selected point along the portage trail. A handheld GPS unit was used to navigate to lakeshore and portage trail transect starting points. Selected campsites were simply marked on our field maps. Transect lengths ranged from 20 m due to an impassable cliff, to ca. 500 m; the latter length was selected as the maximum given that 80% of points within the BWCAW are within 500 m of a lakeshore (Rich, 2005).

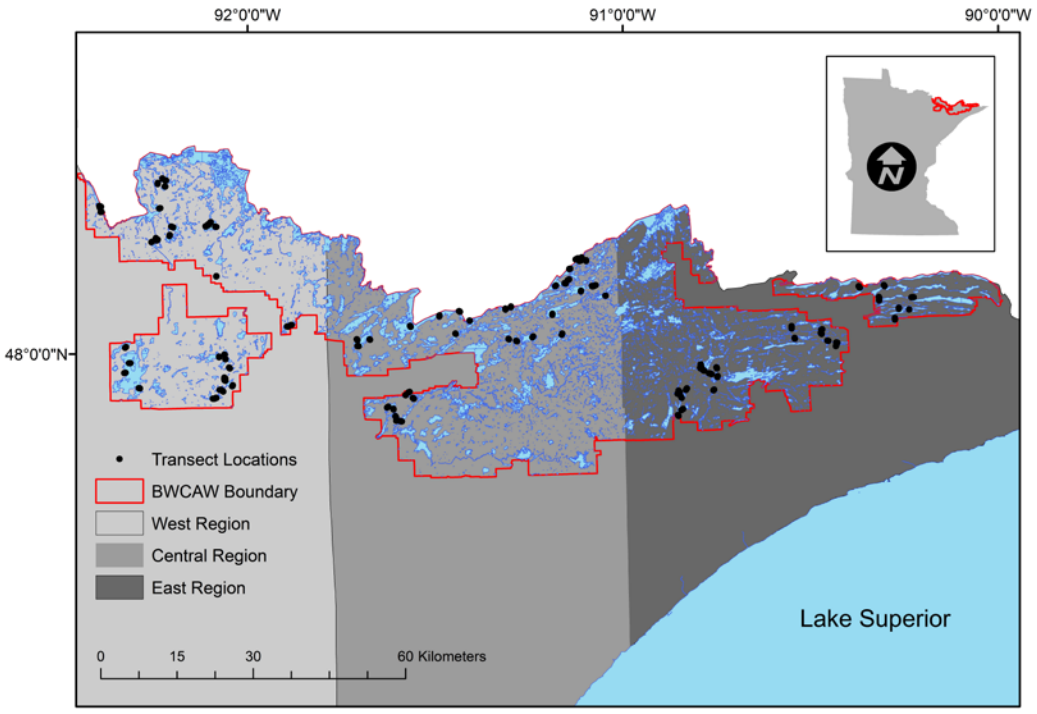


Figure 12: Map of transect locations spanning the longitudinal extent of the BWCAW border.

Study species were grouped into six categories based on tree diameter and/or height: seedlings (< 1.3 m height), small saplings (≥1.3 m height and <2.4 cm d.b.h.), large saplings (2.5 cm to 4.9 cm d.b.h.), small trees (5 cm to 14.9 cm d.b.h.), medium trees (15 cm to 24.9 cm d.b.h.) and large trees (25 cm d.b.h. and over). As the field team advanced along each transect, one researcher trained in northern temperate and boreal tree species identification scanned the forest for the study species, visually estimated size class and took perpendicular horizontal distance measurements from the transect line using a laser rangefinder and compass. The same researcher conducted all observations across all 100 transects to avoid inter-observer variability that would need to be accounted for in modeling. Geospatial data layers of campsite and portage trail locations were obtained from the United States Forest Service (fs.usda.gov/superior, recreation.gov). Lakes, county boundaries, and a legislative boundary for the BWCAW were obtained from the State of Minnesota Geospatial Information Office (gisdata.mn.gov).

Data analysis

Abundance (N) estimates were generated using the Distance package in R (Miller et al. 2017, R Development Core Team, 2018). Abundance is estimated using the equation, $N = n \times A/2wLP_a$, where n = the number of observations, w = transect half-width, L = total transect length, P_a = the proportion of study species detected within the transect area, and A is the area of the study region (Buckland et al., 2000).

P_a is estimated by fitting a detection function, which models the relationship between the horizontal distance from the transect line and the probability of visual detection. Two key assumptions that underlie the fitting of detection functions are that

observers should be able to see objects directly on the line as well as objects near the line with a high probability, and that the probability of visual detection should decrease with increasing distance. Given these assumptions, two properties expected of models for detection functions are a wide shoulder, or relatively flat detection probabilities near 1 and at short distances, and non-increasing probabilities of detection with increasing distance.

The first phase of data analysis involved assessing the distribution of distance measurements for different size classes of each study species to determine if the above-mentioned assumptions were met. From there we moved into a second phase of model selection, where the primary objective was determining the best fitting detection function for different size classes of each study species. The data included in the model for each size class were truncated to a maximum visual detection distance of *w* based on a visual inspection of histograms of the frequency of observations at different distances. The Distance package in R allows the user to choose between three key functions (uniform, half-normal, and hazard-rate) that determine the shape of the detection function model. Model fitting followed the standard "key functions plus adjustments" approach, using the default cosine adjustment term across all three key functions for each species and size class (Miller et al., 2017). The Distance package also allows for the addition of covariates in modeling, so study region was tested for inclusion as part of the model fitting process. The Cramer-von Mises test of goodness of fit was used to determine model plausibility, with a significant test result (p-value <= 0.05) indicating that the model does not fit the data well and should be discarded. Minimization of Akaike's

Information Criterion (AIC) was used to select the top-performing model for each species and size class.

We compared our estimates with estimates derived from FIA data using the United States Forest Service Analysis Tool for Inventory and Monitoring (ATIM) coupled with the Spatial Intersection Tool (SIT) (https://www.fia.fs.fed.us/tools-data). The SIT tool was first used to identify FIA survey plots located within the BWCAW. The ATIM tool was then used to create a report of the number of growing stock trees (at least 5 inches d.b.h.) by species group and diameter class within the BWCAW using data from the 2011-2015 measurement years.

Results

A total of 16,400 observations of our study species were recorded across 100 transects. Eighty-seven percent of observations were red maple (n=14,344) and 9% were northern red oak (n=1,536). Limited occurrences of yellow birch (n=240), green ash (n=183), American elm (n=48), bur oak (n=16), northern pin oak (n=15), silver maple (n=15) and black ash (n=3) were also observed (Figure 13). There were no observations of American basswood.

Figure 13: Number of observations by species. AE=American elm, BA=Black ash, BO=Bur oak, GA=Green ash, NPO=Northern pin oak, NRO=Northern red oak, RM=Red maple, SM=Silver maple, YB=Yellow birch.

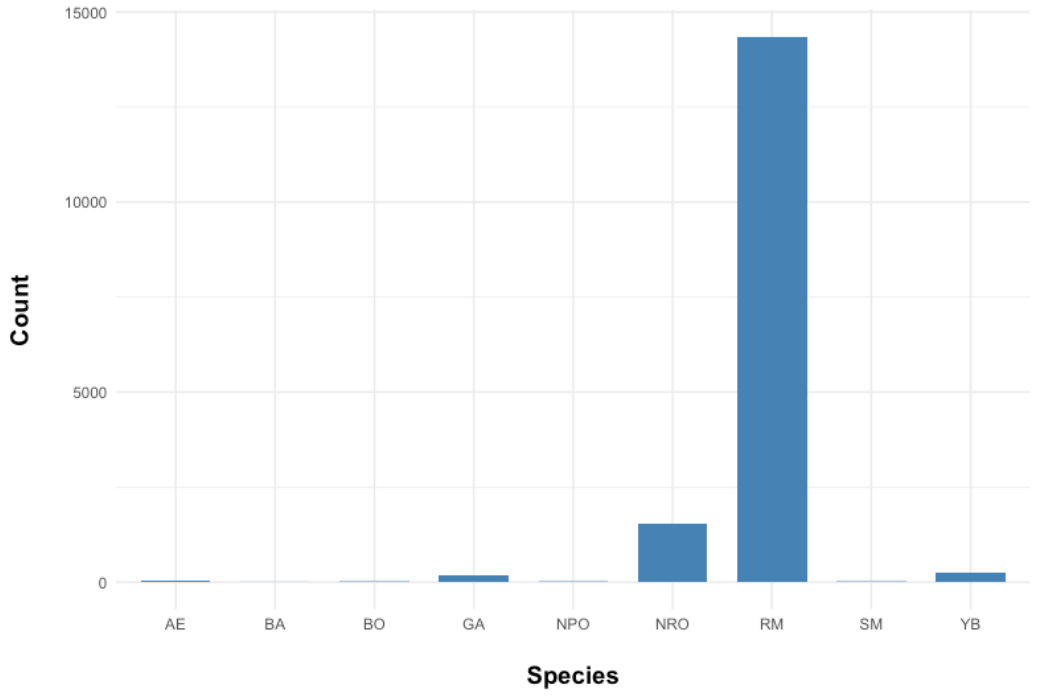
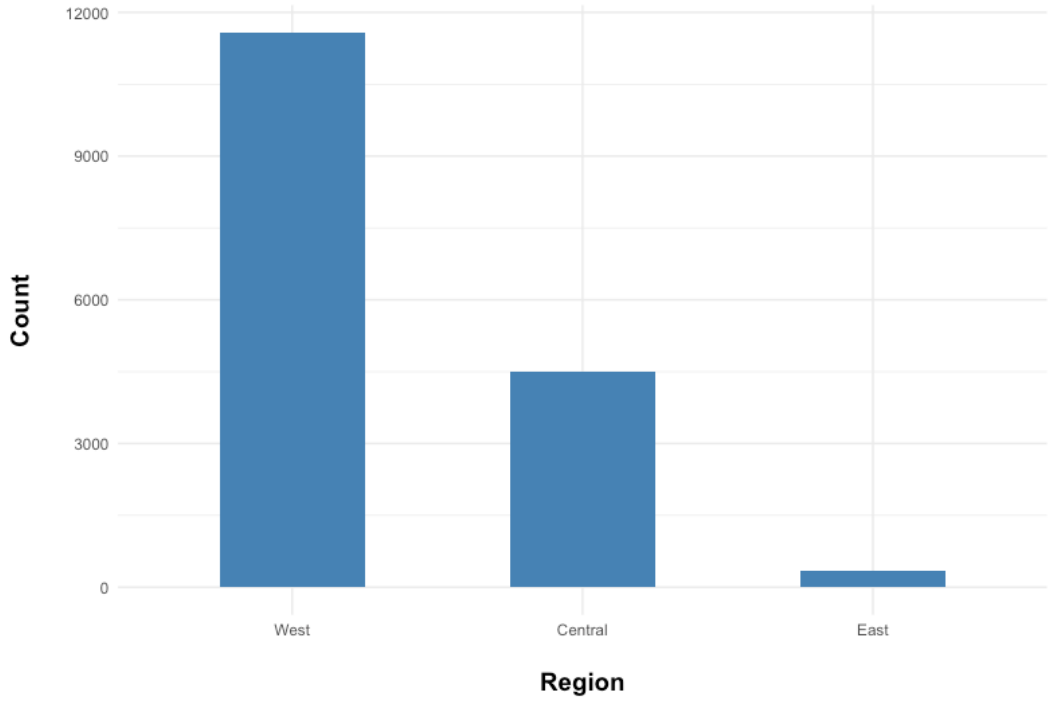


Figure 14: Number of observations by Region.



Seventy percent of observations occurred in the western region (n=11,579), 27% in the central region (n=4,488) and .02% in the eastern region (n=333) (Figure 14). Twenty percent of observations were seedlings < 1.3 m height (n=3,320), 42% small saplings ≥1.3 m height and <2.4 cm d.b.h. (n=6,919), 11% large saplings 2.5 cm to 4.9 cm d.b.h. (n=1,874), 20% small trees 5 cm to 14.9 cm d.b.h. (n=3,232), 0.1 percent medium trees 15 cm to 24.9 cm d.b.h. (n=741), and 0.02% large trees 25 cm d.b.h. and over (n=314) (Figure 15).

Figure 15: Number of observations by size class.

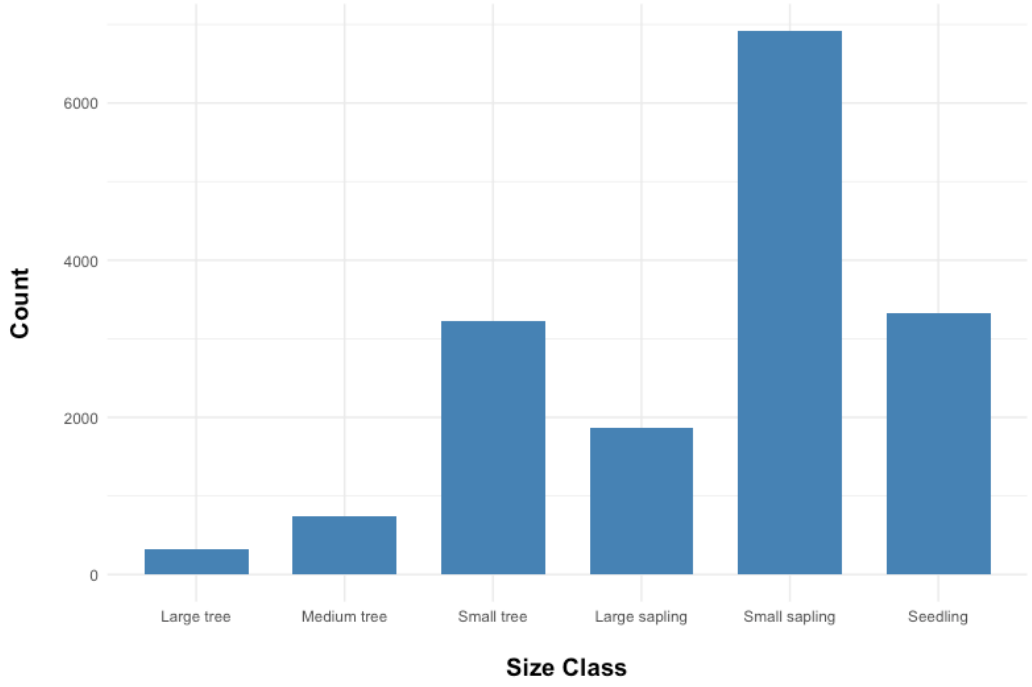
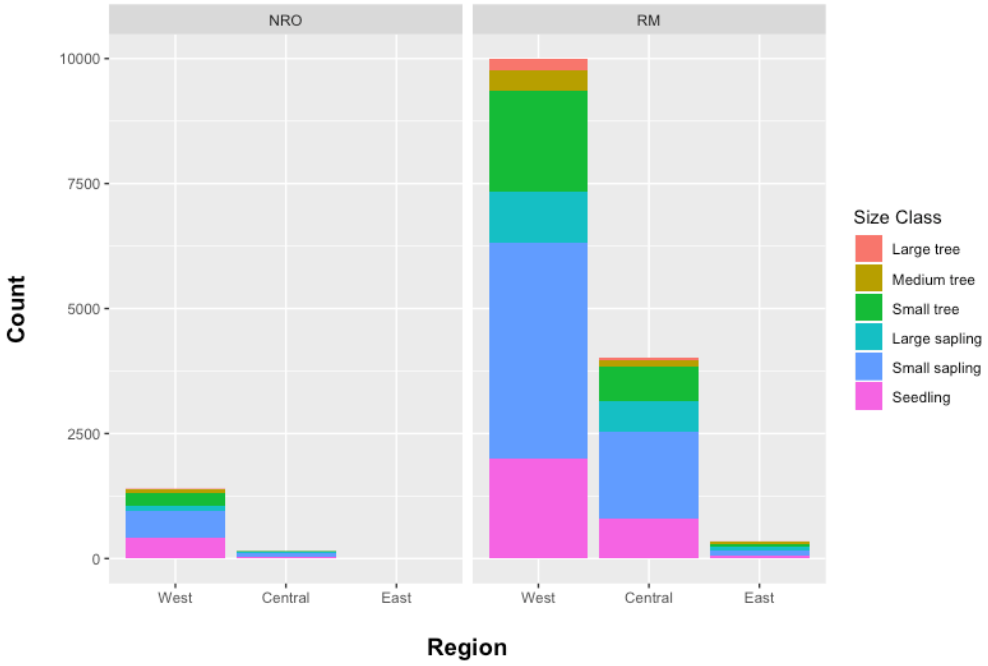
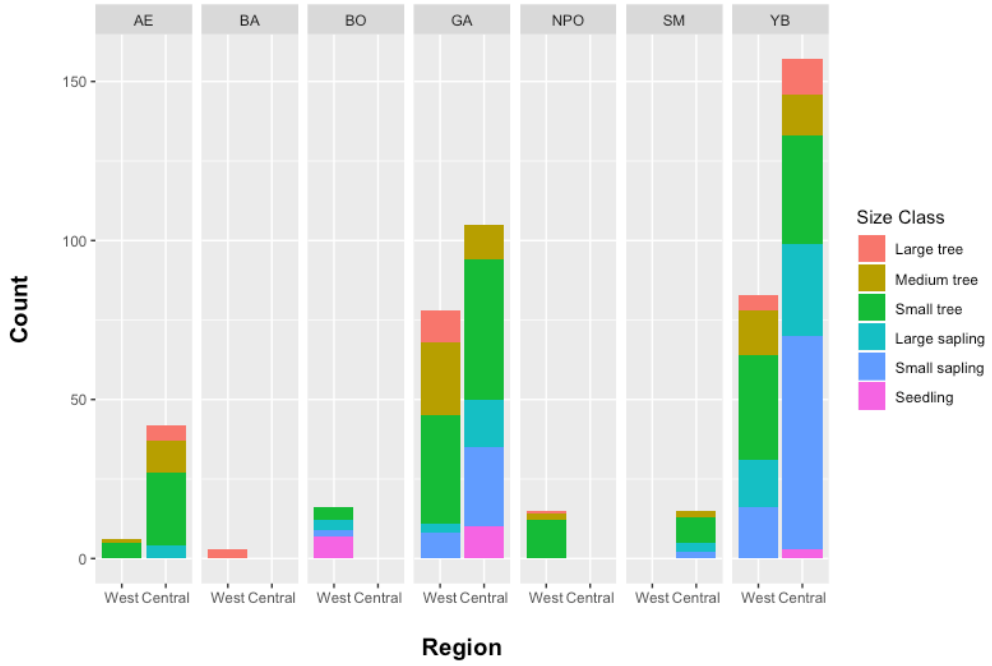


Figure 16: Number of observations by species, size class and region. NRO=Northern red oak and RM=Red maple.



Red maple and northern red oak exhibited a strong west to east trend across all size classes with the highest number of observations in the western region followed by the central and eastern regions respectively (Figure 16, Table 3). American elm, green ash and yellow birch observations were highest in the central region, followed by the western region. Black ash, bur oak and northern pin oak were only observed in the western region. Silver maple was only observed in the central region. No species other than red maple was observed in the eastern region (Figure 17).

Figure 17: Number of observations by species, size class and region. AE=American elm, BA=Black ash, BO=Bur oak, GA=Green ash, NPO=Northern pin oak, SM=Silver maple, YB=Yellow birch.



Distance models and abundance estimates

After assessing the distribution of distance measurements for each study species during the first phase of data analysis, we encountered what is commonly referred to as "spiked data" in the smaller size classes. Spiked data features a distribution of distance measurements characterized by an L-shaped pattern with high detection probabilities directly on the transect line that then quickly declines and flattens with increasing distance. Such a distribution defies one of the key assumptions and characteristics of detection functions discussed above in the data analysis section, which can lead to highly variable and inaccurate estimates of density and abundance. As a result, we focused our modeling efforts on the large and medium tree size classes. We also encountered similar spiked distance distributions from green ash across all size classes, which prevented modeling of that species. Finally, an insufficient number of observations of American

elm, bur oak, northern pin oak, silver maple, and black ash, and zero observations of American basswood, prevented distance modeling of these six species.

Distance models were successfully fit for the large and medium tree size classes of red maple, northern red oak and yellow birch, from which estimates of abundance were generated (Table 3). All three key functions were used across the three study species, with no or single cosine adjustments included. In instances where sufficient observations existed in at least two study regions, models that pooled observations across regions outperformed region specific models and models with region as a covariate.

Abundance estimates from FIA data were limited to the entire BWCAW. As such, comparisons to distance based estimates of abundance are limited to the total study area, without region specific comparisons. It should also be noted that FIA data groups some species in its reporting. Red maple is included in the "soft maple" species group and northern red oak is included in the "select red oaks" species group. Despite these groupings with other species, we were comfortable that abundance estimates for these two species groups were accurate proxies for red maple and northern red oak respectively. Given the extremely low abundance of silver maple, which is the only other "soft maple" present in the BWCAW, it is likely that the vast majority of the "soft maple" category is represented by red maple. In addition to northern red oak, the "select red oak" group includes cherrybark oak and Shumard oak, neither of which is present as far north as the BWCAW.

Red maple

Abundance estimates for large and medium red maple trees in the BWCAW were 1,867,957 and 4,904,190 respectively. When broken down by study region, abundance

estimates for large and medium red maple trees in the western region were 114% and 83% greater than the central region, and 193% and 166% greater than the eastern region, respectively. Distance abundance estimates for large and medium red maple trees were 91% and 28% greater than comparable FIA abundance estimates, and with lower coefficients of variation (Table 3).

Northern red oak

Insufficient northern red oak observations in the central region, and zero observations in the eastern region limited modeling to the western region. Abundance estimates for large and medium northern red oak trees in the western region of the BWCAW were 86,517 and 567,693 respectively. Distance abundance estimates for large northern red oak trees in the western region were 54% less than an FIA abundance estimate of the same size class for the entire BWCAW, with a lower coefficient of variation. Distance abundance estimates for medium northern red oak trees in the western region were 98% greater than an FIA abundance estimate of the same size class for the entire BWCAW, with a lower coefficient of variation.

Yellow birch

Zero yellow birch observations in the eastern region, limited modeling to the western and central regions. Additionally, issues with the distribution of distance measurements in the large tree size class limited estimates to the medium tree size class. The Abundance estimate for medium yellow birch trees in the BWCAW was 196,711, which was 56% less than comparable FIA abundance estimates, with a lower coefficient of variation.

Table 3: Abundance estimates from selected Distance models for Red maple (RM), Northern red oak (NRO) and Yellow birch (YB) across large tree (LT) and medium tree (MT) size classes. Comparative FIA abundance estimates are derived from Forest Inventory and Analysis plots within the BWCAW. Hn=Half-normal key function, Hn/C=Half=normal key function with one cosine adjustment, Hr=Hazard-rate key function, Hr/C=Hazard-rate key function with one cosine adjustment, Uni/C=Uniform key function with one cosine adjustment.

Region	Species	Size Class	Distance Model Parameters				Distance Abundance estimate			FIA Abundance estimate		
			Key function	Formula	C-vM *p*-value	AIC	(trees/ area)	se	% CV	(trees/ area)	se	% CV
West Region	RM	LT					1,447,025	309,860	21.41			
Central Region	RM	LT					395,296	120,421	30.46			
East Region	RM	LT					25,636	19,971	77.9			
Total BWCA	RM	LT	Hn	~1	0.223	1600.69	1,867,957	337,027	18.04	698,782	29,0820	41.62
West Region	RM	MT					3,266,758	648,639	19.86			
Central Region	RM	MT					1,338,176	315,622	23.59			
East Region	RM	MT					299,256	164,642	55.02			
Total BWCA	RM	MT	Hn/C	~1	0.078	3488.83	4,904,190	754,502	15.38	3,664,535	912,833	24.91
West Region	RM	LT+MT					4,697,921	891,412	18.97			
Central Region	RM	LT+MT					1,705,934	406,753	23.84			
East Region	RM	LT+MT					312,046	171,186	54.86			
Total BWCA	RM	LT+MT	Hr/C	~1	0.064	5094.27	6,715,900	1,006,785	14.99	4,363,317	935,368	21.44
West Region	NRO	LT	Uni/C	~1	0.929	60.57	86,517	57,922	66.95			
Central Region	NRO	LT					N/A	N/A	N/A			
East Region	NRO	LT					N/A	N/A	N/A			
Total BWCA	NRO	LT					N/A	N/A	N/A	150,682	139,599	92.64
West Region	NRO	MT	Hr	~1	0.863	356.15	567,693	261,494	46.06			
Central Region	NRO	MT					N/A	N/A	N/A			
East Region	NRO	MT					N/A	N/A	N/A			
Total BWCA	NRO	MT					N/A	N/A	N/A	192,815	148,899	77.22
West Region	NRO	LT+MT	Hr	~1	0.905	393.08	652,328	310,848	47.65			
Central Region	NRO	LT+MT					N/A	N/A	N/A			
East Region	NRO	LT+MT					N/A	N/A	N/A			
Total BWCA	NRO	LT+MT					N/A	N/A	N/A	343,498	282,434	82.22
West Region	YB	MT					94,776	71,737	75.69			
Central Region	YB	MT					101,935	101,936	100.00			
East Region	YB	MT					N/A	N/A	N/A			
Total BWCA	YB	MT	Uni/C	~1	0.782	158.01	N/A	N/A	N/A	351,592	268,925	76.49
West Region	YB	LT+MT					102,754	82,678	80.46			
Central Region	YB	LT+MT					150,337	150,098	99.84			
East Region	YB	LT+MT					N/A	N/A	N/A			
Total BWCA	YB	LT+MT	Uni/C	~1	0.424	268.86	N/A	N/A	N/A	552,502	393,045	71.14

Discussion

The objective of this research was to improve our understanding of how well poised the forests of the BWCAW are to transition from a boreal to a temperate dominated forest type under climate change. To that end, we assessed the abundance and spatial distribution of temperate tree species currently at low abundances in the wilderness, but whose populations are expected to increase to under climate change. We hypothesized that: 1) red maple and northern red oak would be the most abundant temperate species in the BWCAW, 2) our abundance estimates for all temperate tree species in the BWCAW would be higher than FIA-derived estimates, and 3) the spatial distribution of temperate tree species in would closely follow a west to east summer temperate gradient.

Our results indicate that red maple is by far the most abundant northern temperate tree species currently present within the BWCAW across all size classes. Estimates of abundance for large and medium red maple trees were an order of magnitude greater than northern red oak, the second most abundant species in our study. Results also indicate that the spatial distribution of red maple abundance in the BWCAW is correlated with the west to east 2°C summer temperature gradient that spans the wilderness.

Red maple has been known to be a minor component of BWCAW forests for decades, based on early plant community classification work in the wilderness by Ohmann and Ream (Ohmann and Ream, 1971). An unfavorable climate and pre-settlement disturbance regime that favored cold and fire adapted boreal species have historically kept red maple abundance at low levels. Red maple's northern range boundary within the BWCAW coincides with the -40°C mean minimum isotherm, the

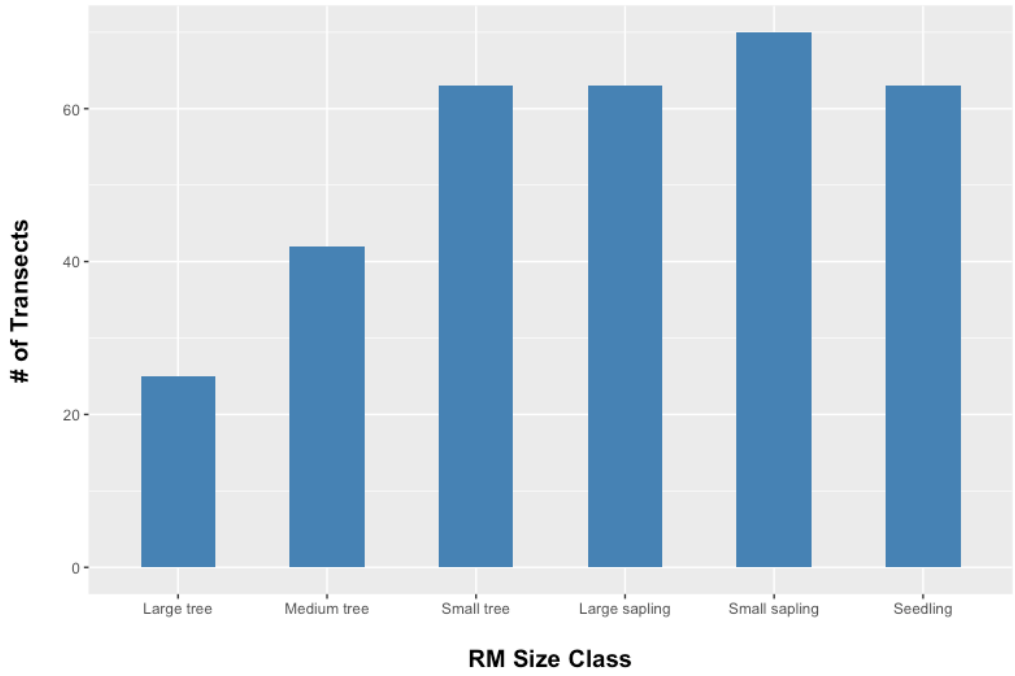
temperature at which freezing damage to its cells can occur. While adult red maple trees can stump sprout after fire and colonize recently burned sites via wind dispersal of dual-winged seeds, red maple is a very fire sensitive species (Peroni, 1994).

Historically, fires of varying intensity, size and frequency in the BWCAW interacted with a varying topography over long periods of time to create a patchwork of boreal forest types and age-classes (Heinselman, 1996). Large-scale crown fires or high-intensity surface fires with rotation periods of 50-100 years resulted in a mosaic of pure and mixed stands of jack pine, black spruce, quaking aspen, paper birch, balsam fir and white spruce (Heinselman, 1996). Intermittent, low-intensity surface fires with return intervals of 5 to 50 years resulted in stands of white and red pine (Heinselman, 1996). Nearly the entire 440,000 ha area that now comprises the BWCAW was burned one to several times between the years 1595 to 1972, (Heinselman, 1996). This pre-settlement fire regime combined with low abundance of reproductive adult red maple trees, prevented shade-tolerant red maple seedlings and saplings from becoming established in the understory, making the species an inferior successional competitor with dominant boreal species.

Over the past century fire suppression and land fragmentation to the south have lengthened fire recurrence intervals in the BWCAW to greater than 700 years, allowing shade-tolerant red maple seedlings and saplings to become more established in the understory (Abrams, 1998). Further, an increased incidence of wind disturbance in the BWCAW makes red maple better poised to respond to release from suppression and ascend into the canopy. At the same time, climate change has resulted in warmer summer temperatures, and fewer extreme low winter temperature events (-40°C) at red

maple's northern range boundary in northern Minnesota (Midwestern Regional Climate Center). While no historical estimates of red maple abundance in the BWCAW exist with which to compare our results, we did find that red maple seedlings, saplings and small trees occurred over a larger area than medium and large trees (Figure 18).

Figure 18: Number of transects (n=100) where red maple was observed by size class. Observations have been limited to a maximum distance of 5 m given differences in visual detection probabilities across size classes at increasing distance from the transect line.



Other empirical studies in the region would also seem to support our conclusion that red maple abundance in the BWCAW is increasing as a result of changes in climate and disturbance. Increasing average summer temperatures have resulted in increased red maple sapling growth rates, facilitating red maple expansion into adjacent patches of southern boreal forest in northern Minnesota (Fisichelli et al., 2013). A similar positive relationship between increased temperature and red maple sapling growth rates at sites in northern Minnesota near the BWCAW (Reich et al. 2015). Moreover, red maple sapling survival seems to be less sensitive to temperature than does growth rate (Reich et al.,

2015). While we were not able to develop distance models and abundance estimates for red maple seedlings, saplings and small trees due to previously discussed spiked data limitations, observed abundances for these three size classes showed a similar west to east spatial distribution pattern as medium and large red maple trees (Figure 19, Figure 20, Figure 21).

Figure 19: Number of red maple seedlings per unit transect length. Only observations directly on the transect line (distance = 0 / probability of detection = 1) included to ensure equal detection probabilities among transects.

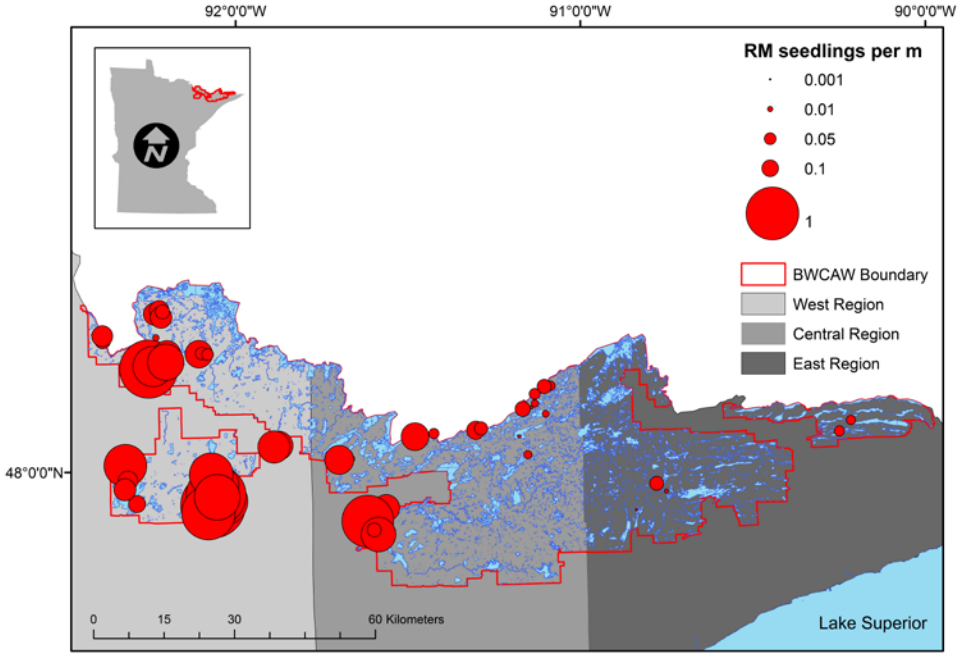


Figure 20: Number of red maple saplings per unit transect length. Only observations directly on the transect line (distance = 0 / probability of detection = 1) included to ensure equal detection probabilities among transects.

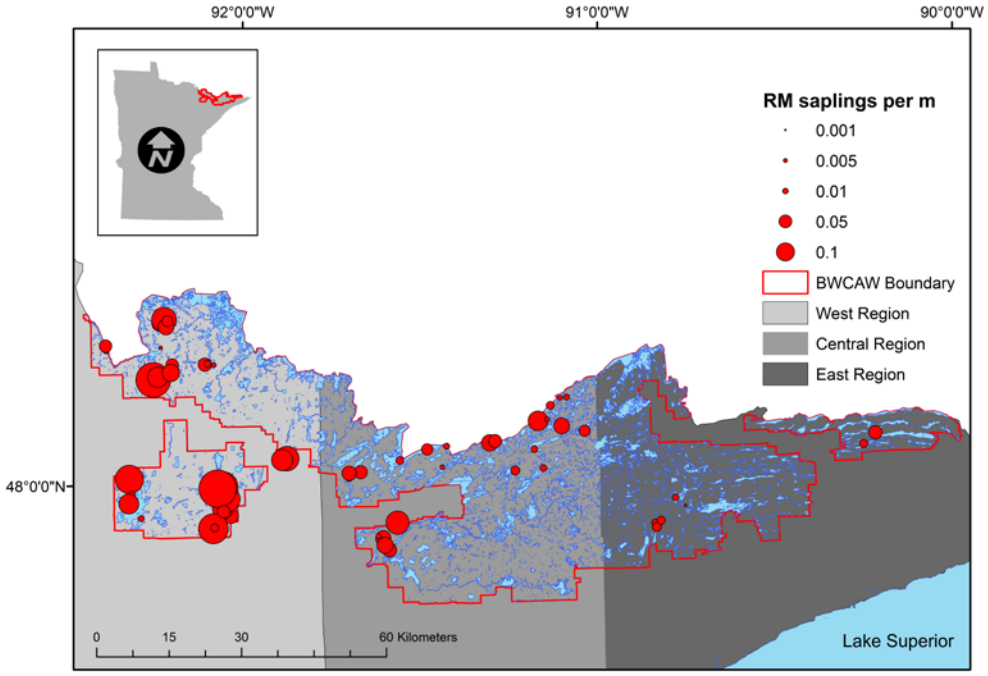
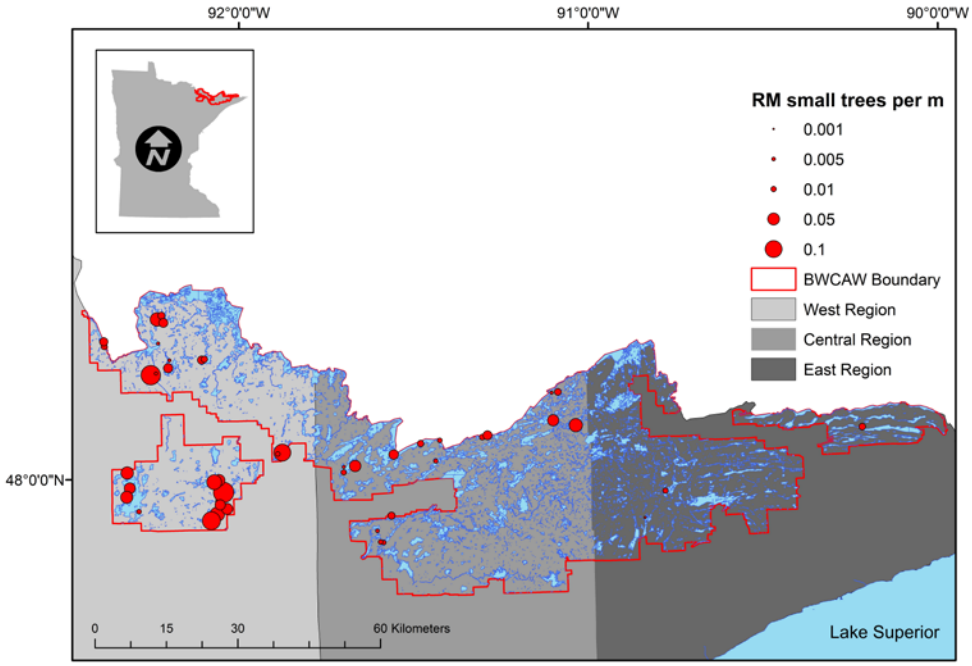


Figure 21: Number of red maple small trees per unit transect length. Only observations directly on the transect line (distance = 0 / probability of detection = 1) included to ensure equal detection probabilities among transects.



Our estimates of large and medium red maple tree abundance in the BWCAW were significantly higher than comparable estimates using FIA data (Table 3). Our estimates were also ostensibly more accurate based on lower coefficients of variation. While grid-based plot surveys like the FIA program are very effective in generating accurate abundance estimates for dominant and co-dominant species, they have been shown to underestimate the occurrence of rare species (Kissa and Sheil, 2012). The spatial distributions of low abundance species are often quite patchy across the landscape and thus easily missed by more traditional fixed plot survey designs (Buckland et al., 2007). By using the distance survey method, we were able to cover more ground across the BWCAW and determine that red maple abundance is likely higher in the wilderness than previously known.

Northern red oak was the second most abundant northern temperate species within the BWCAW across all size classes. Alongside red maple, northern red oak has been a minor component of the BWCAW landscape for some time (Ohmann and Ream, 1971). No historical estimates of northern red oak abundance within the BWCAW exist, but like red maple, northern red oak has expanded its range into the southern boreal forests of northern Minnesota, facilitated by increasing average summer temperatures (Fisichelli et al., 2013). Our estimate of large northern red oak tree abundance in the BWCAW was lower than comparable FIA estimates, but our estimate of medium northern red oak trees was significantly higher than FIA estimates. Our estimates for both size classes had a lower coefficient of variation indicating more accurate results, however coefficients of variation values for both data sources were quite high and thus results should be interpreted with caution (Table 3).

Observations of American basswood, bur oak, northern pin oak, green ash, American elm, silver maple and yellow birch were orders of magnitude lower than red maple and northern red oak, or absent altogether. At 440,000 ha, the BWCAW is a large study area, and it is almost certain that our survey missed existing populations of all other study species. Our survey also did not include areas further south of the BWCAW border where abundances of other study species may be higher, and from which successful migration into the BWCAW may occur under climate change. However, given the previously discussed disparity between historical tree migration rates and the velocity of climate change in this region, our results indicate that red maple and northern red oak are the two northern temperate tree species best poised at present to expand their northern ranges within the BWCAW. In addition to their current abundance on the landscape, both red maple and northern red oak are capable of high seed production and relatively long-range seed dispersal compared to other northern temperate species. Red maple seed dispersal is wind-aided via dual-winged samaras and dispersal of northern red oak acorns can be facilitated by blue jays (*Cyanocitta cristata* L.), which have been shown to transport and cache acorns up to 1.9 km from seed trees (Peroni, 1994; Johnson and Webb, 1989; Darley-Hill and Johnson, 1981). Under a future fully temperate climate in the BWCAW, red maple and northern red oak could form new forests. Additional research on seed production rates at their far northern range as compared more southerly locations would help determine whether seed production is sufficient to support a forest transition. Assuming sufficient seed production, there could still be a substantial time lag before other northern temperate species were able to migrate north, assuming those

species are able to keep pace with the rate of climate change, and therefore tree species diversity in the BWCAW would likely be low for decades to a few centuries.

Of course, abundance and dispersal ability will not be the only factors that determine colonization success of red maple and northern red oak in the BWCAW. Fisichelli et al. (2012) also found that at sites in northern Minnesota with high deer densities, any temperature facilitated expansion of temperate tree species was "cooled," or inhibited by herbivory, and they also found that sites invaded by earthworms showed similar understory effects. This led the authors to conclude that high deer densities and the spread of exotic earthworms may delay the migration of temperate trees northward while favoring boreal tree species due to reduced competition. Approximately 33 percent of forestland in the BWCAW is predicted to be invaded by earthworms at present (Chapter 1), and deer populations are expected to increase in the wilderness with a warming climate.

Study limitations and areas of further research should be noted. By using line transect distance sampling, our study was able to cover more area than comparable FIA plots, however our total survey area still represents a small fraction of the landscape. Survey intensity should have been higher in the eastern region of the BWCAW, where northern temperate tree species are currently least abundant. As previously noted, our study does not account for populations of northern temperate tree species immediately to the south that may be able to keep pace with climate change and successfully colonize a future warmer BWCAW. Additional fine-resolution surveys of northern temperate tree species both in and near the southern border of BWCAW would further aid climate change adaptation planning for the wilderness. Also helpful, would be long-term

demographic studies of both boreal and northern temperate tree species in the region to track observed shifts in spatial distribution across size classes, evidence for which is currently limited in the literature (Beckage et al., 2008).

Conclusions

Climate change presents an unprecedented threat to the forests of the BWCAW that will not be mitigated by federal protection (Frelich and Reich, 2009). The boreal tree species that currently dominate the BWCAW landscape, and contribute to its ecological, cultural and recreational values, are projected to retreat to the northeast, potentially out of the wilderness and Minnesota altogether by the end of the century. Given the velocity of future climate change and the unprecedented corresponding rates at which northern temperate tree species would need to migrate to keep pace, it remains unclear if a successful boreal to temperate forest transition can occur within the BWCAW without intervention. While our results indicate that current abundance of red maple seed sources are high, our estimates of northern red oak abundance were highly variable, and we found little to no evidence of substantial seed sources for other northern temperate tree species within the wilderness boundary. Further surveys of northern temperate seed sources within and near the BWCAW will be critical for future adaptation efforts, and the facilitated migration of northern temperate tree species with little to no current abundance may be necessary to maintain a diverse, forested landscape in the wilderness under a future warmer climate.

Relative understory abundance of boreal and temperate tree species in the forests of the Boundary Waters Canoe Area Wilderness (U.S.A.)

Introduction

Climate change is predicted to catalyze a redistribution of tree species ranges and forest types across northern Minnesota by the end of the century (Duveneck et al., 2014; Frelich and Reich, 2009; Galatowitsch et al., 2009). Climate change projections for northern Minnesota include increased temperatures, stable to decreasing precipitation, and a resulting decrease in precipitation-to-evaporation ratios, resulting in warmer and drier conditions. Such conditions are expected to result in a northeasterly shift in the prairie-forest and boreal-temperate forest ecotones in northern Minnesota, as has occurred during past episodes of warming (Frelich and Reich, 2009; Davis and Shaw, 2001). Northward shifts in suitable tree species habitat ranging from 100 km to 500 km per century are projected to occur, significantly exceeding estimates of past range shifts in this region of 20 km to 40 km per century during the mid-Holocene warm period (Galatowitsch et al., 2009; Davis and Shaw, 2001). These projections present a complex and unplanned for variable in contemporary management of the forests of the Boundary Waters Canoe Area Wilderness (BWCAW), and requisite efforts to "protect and enhance the natural values…of the wilderness" (Frelich and Reich, 2009; BWCAW Act, 1978; Wilderness Act, 1964).

Several studies have modeled future climate change induced tree species range shifts in northern Minnesota to aid in adaptation planning efforts (Swanston et al., 2018; Duveneck et al., 2014; Ravenscroft et al., 2010; Xu et al., 2010; Galatowitsch et al., 2009; Iverson and Prasad, 2007; Walker et al., 2002). Results show strong agreement in

projecting declines in suitable habitat and relative abundance of boreal tree species that currently dominate the BWCAW landscape including black spruce (*Picea mariana),* balsam fir (*Abies balsamea),* quaking aspen (*Populus tremuloides),* paper birch (*Betula papyrifera),* and jack pine *(Pinus banksiana*). Results also show strong agreement in projecting increases in suitable habitat and relative abundance for northern temperate deciduous tree species currently at low abundances in the BWCAW including: American basswood (*Tilia americana*), northern red oak (*Quercus rubra,* declines under high emissions), bur oak (*Quercus macrocarpa*), green ash (*Fraxinus pennsylvannica*), American elm (*Ulmus americana*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis,* declines under high emissions).

Empirical studies in the region have begun to find supporting evidence for future climate change induced tree species range shifts in northern Minnesota. Reich et al. investigated the impacts of experimental warming (+3.4°C) on the performance of juveniles of 11 boreal and northern temperate tree species that co-occur within the boreal-temperate forest ecotone by measuring the carbon gain and growth of over 4,100 juvenile trees over three growing seasons at two sites in northern Minnesota near the BWCAW. For boreal species, they found net photosynthetic carbon gain and growth were adversely impacted by warming, with balsam fir and white spruce (*Picea glauca*) experiencing the most significant declines. Conversely, they found net photosynthetic carbon gain and growth of temperature juvenile trees was increased by warming, with maple and oak species exhibiting the greatest gains (Reich et al., 2015). Similarly, Fisichelli et al. found that increasing average summer temperatures have resulted in increased northern temperate sapling growth rates across northern Minnesota, Wisconsin and Upper

Michigan, facilitating temperate expansion into adjacent patches of southern boreal forest (Fisichelli et al., 2013).

However, Fisichelli et al., also found that a multitude of interrelated tree regeneration drivers including, but not limited to climate, will need to be accounted for in understanding and predicting future tree species range shifts in the region. Their results showed that climate, understory environment, overstory composition and understory biota were all significantly associated with variations in tree regeneration performance in mixed temperate-boreal forests across the upper Midwest. In a companion study, the same authors found that at sites in northern Minnesota with high deer densities, any temperature facilitated expansion of temperate tree species was "cooled," or inhibited by herbivory of temperate species, giving boreal species that are generally less palatable to deer a competitive advantage (Fisichelli et al., 2012). Earthworms have been shown to have a similar relative effect, creating bare mineral soil seedbed conditions that favor fire-adapted boreal species in mixed boreal-temperate forests (Frelich et al., 2012).

In addition to their direct impacts on understory biodiversity, earthworms are also expected to influence forest compositional shifts within the temperate-boreal ecotone in response to climate change (Fisichelli et al. 2012). The bare and compacted mineral soil surface created by earthworms increases evaporative losses of soil moisture and decreases infiltration of precipitation (Frelich et al. 2006). Combined with increasing temperatures, this creates warmer and drier soils that favor drought tolerant species able to germinate on bare mineral soil (Eisenhauer et al. 2011). These conditions strongly disfavor sugar maple (*Acer saccharum),* possibly creating a competitive advantage for other temperate species including red maple and northern red oak (Frelich et al 2012).

Because all boreal tree species are able to germinate on bare mineral soil, and deer preferentially browse temperate tree seedlings over boreal seedlings, some researchers have concluded that earthworms may delay the migration of temperate trees northward while favoring boreal tree species resistance due to reduced competition (Fisichelli et al. 2012; Frelich et al. 2012; Fisichelli et al. 2013). However, in a recent microcosm study, nightcrawlers reduced germination rates of boreal tree species including balsam fir, white spruce, black spruce and jack pine, and reduced survival rates of balsam fir and white spruce seedlings (Drouin et al. 2014). Approximately 33 percent of forestland in the BWCAW is predicted to be invaded by earthworms at present (Chapter 1).

Topography also impacts on soil moisture potential at the stand scale in the BWCAW and may also play an important role determining understory regeneration trends in a warmer climate. Danz et al., found that "climate," defined as Precipitation (P) – Potential Evapotranspiration (PET), was the "ultimate" control over the location of the prairie-forest border in Minnesota, particularly when examined at larger spatial scales (Danz et al., 2011). The authors also found that topography was an important factor in determining the location of the boundary at finer spatial scales. Empirical studies have shown that ample soil moisture can also allow trees to grow on sites that would otherwise be outside the bounds of their temperature optimum, which can lead to over and/or under estimates of tree species range shifts using climate envelope models alone (McLaughlin and Zaraleta, 2011).

Given the unprecedented velocity of projected future climate change in the region, the comparatively slow pace of historical tree migrations during previous episodes of climate warming, and the significant ecological, cultural and recreational value of the

BWCAW, it is important that future management decisions be informed by landscape-level data where possible. To that end, the purpose of this study was to improve our understanding of how temperature, overstory composition, soil moisture potential and earthworm invasion are currently impacting understory regeneration trends in the boreal forests of the BWCAW to aid in future climate-change adaptation planning efforts for the wilderness. To do so, we assessed the impact of seasonal temperature, overstory composition, degree of earthworm invasion and soil moisture potential on the relative understory abundance of ten boreal and northern temperate tree species currently present in the BWCAW. We hypothesized that: 1) higher average summer temperatures would be negatively related to understory regeneration of boreal species and positively related for temperate species, 2) increased soil moisture potential would be positively related to understory boreal regeneration, possibly ameliorating the effects of higher site-specific summer temperatures, and 3) degree of earthworm invasion would be positively related to understory regeneration of boreal species and negatively related for temperate species.

Methods

Study area

The BWCAW is a 400,000 ha, paddle-only federal Wilderness area located within the Superior National Forest in far northeastern Minnesota, USA. Its forests have been described as "near boreal," with fires of varying intensity and frequency creating a patchwork of pure and mixed stands of boreal tree species including jack pine, black spruce balsam fir, quaking aspen, paper birch and white spruce. Red pine (*Pinus resinosa)* and eastern white pine (*Pinus strobus)* stands are often found on leeward lakeshores and islands where fire intensity was typically less, and stands of northern

white cedar (*Thuja occidentalis)* are often found on wet sites (Frelich & Reich 1995; Heinselman 1996). Some northern temperate tree species are also present in the BWCAW, primarily red maple and northern red oak, with some stands found on the western side where summer temperatures are on average 2°C warmer than the eastern side of the wilderness (Ohmann & Ream 1971; Heinselman 1996). A west to east elevation gradient also occurs across the BWCAW, with higher mean elevation in the east. While absolute increases in elevation from west to east across the wilderness are relatively modest, higher elevations combined with a predominant west to east orientation of long slender lakes in the far eastern portion of the BWCAW has created a unique area of steep north slopes that likely experience the coolest and wettest growing season conditions in the wilderness.

The entire BWCAW is underlain by Pre-Cambrian rock, primarily granite but also gabbro, greenstone and some slates. Its soils are the result of sandy and gravelly loam glacial deposits, and soils are generally thin with rocky outcroppings and exposed bedrock common along lakeshores and on ridge tops (Ohmann & Ream 1971). While logging is currently prohibited in the BWCAW, approximately 50% of the area within its current borders was logged between the 1890s and the late 1970s, and logging operations continue along its southern, western and eastern borders (Heinselman, 1996). The BWCAW shares its northern border with Ontario's Quetico Provincial Park, where logging is also prohibited.

Study site selection & sampling

To account for the aforementioned west to east environmental gradients, four study site regions were selected that collectively spanned the longitudinal and latitudinal

extent of the BWCAW, while also offering proximity to reliable year round roads for efficient sensor deployment and biannual data logger downloads and maintenance. The four areas included: 1) Northern Echo Trail area, 2) Fernberg Road area, 3) Sawbill Trail area, and 4) Gunflint Trail area (Figure 22).

Figure 22: Map of study site regions spanning the longitudinal and latitudinal extent of the BWACW.

A total of 108 study sites were established adjacent to, and within, the BWCAW border (Fig 23). Within each region, study sites were stratified by vegetative cover type, slope and aspect, to ensure a representative sample of BWCAW cover and landform types. Two broad cover types comprised the majority of study sites: mixed-boreal conifer and mixed-boreal deciduous, based on Ohmann and Ream's BWCAW plant community types (Ohmann and Ream, 1971). Mixed-boreal conifer sites included jack pine (oak), jack pine (fir), jack pine/black spruce, black spruce/jack pine, eastern white pine, red pine, fir-birch and northern white cedar. Mixed-boreal deciduous sites included aspen-birch and maple/aspen/birch. Six landform types were selected including 1) forested ridge tops (n=24); 2) forested mid-slope northern aspect (n=18, 315 degrees to 45 degrees); 3) forested mid-slope eastern aspect (n=12, 45 degrees to 135 degrees); 4)

forested mid-slope southern aspect (n=15, 135 degrees to 225 degrees); 5) forested mid-slope western aspect (n=12, 225 degrees to 315 degrees); and 6) forested lowland (n=21). For landform types 2 through 5, a mix of slopes between 10% and 40% were selected, a range that comprises approximately 71% of the slopes in the BWCAW based on an analysis of 30 meter DEMs of the region. Several additional study sites were selected that represent less common, but ecologically important landform and cover types in the face of a changing climate. Six mid-slope sites were established on forested north slopes greater that 40% in the Gunflint Trail area to ensure adequate coverage of the unique steep north slopes that occur in that region. Four of the above sites were established in pure stands of northern temperate deciduous species that are predicted to increase in abundance in the BWCAW under climate change including northern red oak (n=2, forested ridge top), red maple (n=1, forested ridge top), and sugar maple (n=1, mid-slope southern aspect). All study sites were considered to be fully stocked stands on soil types typical of the BWCAW, were free of any recent disturbance, such as fire or logging, that could have affected species composition in the understory and overstory layers, and placed far enough from roads to avoid any data bias.

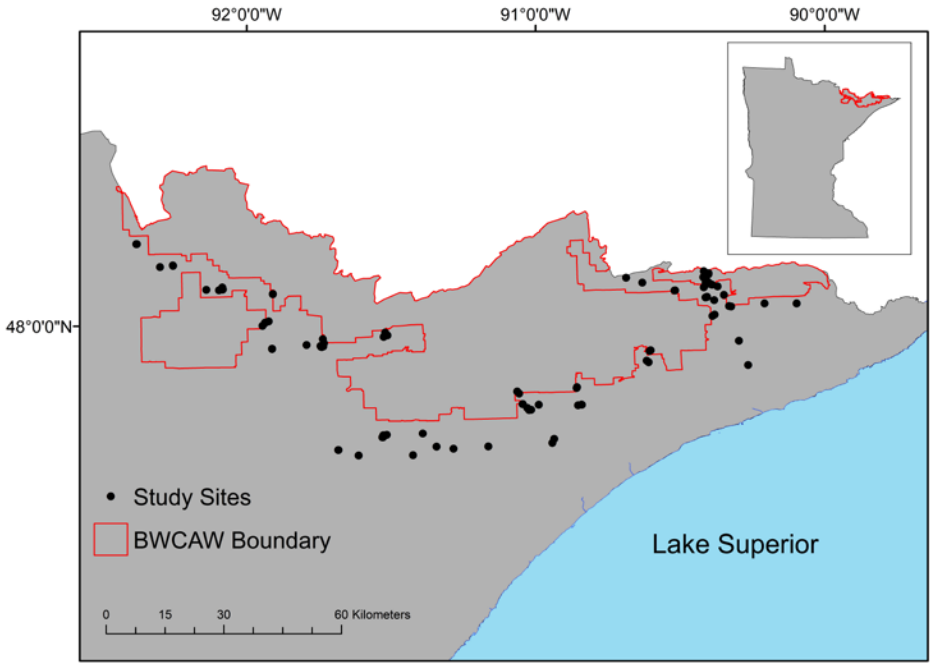


Figure 23: Map of study sites in relation to the BWACW border.

Site temperature data was collected using HOBO pendant data loggers (https://www.onsetcomp.com/products/data-loggers/ua-001-64). The data loggers were deployed at study sites in May 2012 and recorded hourly ambient air temperature measurements for two years. Prior to deployment in the field, the data loggers were tested for accuracy at both high and low temperatures using a growth chamber and ice bath respectively. To minimize direct solar radiation measurement errors, the data loggers were housed inside a solar radiation shield constructed of two inverted and nested white plastic funnels (Fig 24, Hubbart, 2011). The funnels selected for use were made of a sturdy, non-transparent white plastic to maximize albedo. A five-inch diameter funnel was nested within a six-inch diameter funnel. A small piece of poly tubing was placed around the exit point of the inside funnel to prevent it from fully nesting inside the outer funnel, and holes were drilled through the inner funnel to further improve passive air

circulation. White nylon rope was used to hang the data loggers and solar radiation shields on the north side of trees approximately 2 m above the ground. Whenever possible, the sensors were hung from evergreen conifer trees to provide an additional layer of shielding from direct solar radiation (Lundquist & Huggett, 2008). A white plastic disc approximately 3 mm thick and 3 cm in diameter, with a holed drilled in it for the rope to pass through, was used to close off the top of the outer funnel to help keep precipitation out. Temperature data collection was successful at 98 percent of study sites (n=106) across the full 2-year time period. The data loggers at two sites showed signs of tampering and were excluded from analyses.

Figure 24: HOBO pendant temperature data loggers were hung on the north side of trees approximately 2m from the ground inside a solar radiation shield constructed of inverted white plastic funnels. Photo credit: David Chaffin

Site overstory, sapling, seedling and earthworm invasion data were collected within nested fine (3m radius), medium (5m radius), and coarse (12m radius) scale circular plots using the data logger tree as plot center, during the summers of 2012 and

2013. Within the fine scale plots, seedlings ≥10 cm and ≤ 1.3 m in height, and saplings > 1.3 m in height and ≤ 2.5 cm d.b.h. were tallied by species. Within the medium scale plots, all trees > 2.5 cm d.b.h. were surveyed for species and d.b.h., and an earthworm invasion severity index of 1-5 was assigned using the Invasive Earthworm Rapid Assessment Tool protocol (IERAT; Loss et al., 2013). The IERAT is a five-stage earthworm invasion protocol that allows for rapid classification of invasion at a site based on distinct visual signatures left by different earthworm species due to their different feeding and burrowing habits including castings, middens, degree of litter fragmentation, and abundance of fine root presence in the O horizon. The IERAT stages largely correspond to the five sequential stages of earthworm invasion identified in this region by Holdsworth et al. (2007), with the number and types of earthworms as well as the ecological impact increasing with each stage. IERAT stage 1 is presumed to be earthworm free with a fully-intact forest floor. IERAT stage 2 is associated with the onset of invasion by small leaf worms (*D. octaedra)* that live exclusively in the litter layer, feeding on fungi and bacteria with limited impact to the forest floor (Holdsworth et al 2007). IERAT stage 3 is associated with the onset of invasion by beaver tails, *Aporrectodea* and *Octolasion spp.*, the removal of humus (O_a) layer and absence of fine plant roots. IERAT stage 4 is associated with the onset of invasion by nightcrawlers, the removal of leaf litter older than the previous autumn (O_i) and mineral soil (A-horizon) present. IERAT stage 5 is associated with the eventual dominance of nightcrawlers, complete removal of the forest floor (Oi, Oe, Oa) with only mineral soil (A-horizon) present at the surface (Figure 4). Field staff were trained in application of the IERAT by

one of its authors prior to data collection (Loss et al. 2013). The IERAT dichotomous key was used in the field to assign an invasion stage ranking at each study site.

Figure 25: This image taken along a portage trail near the BWCAW shows a stage five invasion with the forest floor completely removed, exposing the roots of a balsam fir. Photo credit: Doug Wallace

Within the coarse scale plots, trees ≥ 5 cm d.b.h. were tallied by species and assigned to one of three size classes based on a visual assessment (≥ 5 cm d.b.h and ≤ 14.9 cm d.b.h., ≥ 15 cm d.b.h. and ≤ 24.9 cm d.b.h., ≥ 25 cm d.b.h). Site overstory basal area was calculated using data from the medium and coarse scale plots. Following the method from Rich et al., continuous d.b.h. measurements from the medium scale plots were used to estimate mean basal area and quadratic mean diameter (QMD) of each species in the three coarse scale size classes. Species and size class QMDs were used to calculate an individual basal area for each tree tallied in the coarse scale plots, which was

then combined with individual basal area measurements from the medium scale plots to calculate total basal area, species specific basal area, conspecific relative basal area and boreal relative basal area (Boreal RBA) for each site (Rich et al., 2007). Tree species included in Boreal RBA calculations were balsam fir, jack pine, paper birch, quaking aspen and white spruce. Compound topographic index (CTI), a proxy for soil moisture potential, was calculated for each site from a 10 m digital elevation model (DEM), which was resampled from a 1 m LiDAR-derived DEM of the region (https://gisdata.mn.gov). Also referred to as a "steady state wetness index" or "wetness index," CTI is calculated as CTI = ln(A/S), where A = flow accumulation and S = slope. CTI provides a measure of potential soil moisture at a site by combining catchment area with slope. Low slope and/or large catchment area indicate higher potential for water to collect (University of Minnesota, Water Resources Center, LiDAR Training Materials). As a point of reference, a maximum CTI value of 8.17 was observed at a lowland northern white cedar site, while a minimum CTI value of -5.98 was observed at a mixed-boreal deciduous site on a 43% slope.

Statistical analyses

Linear mixed-effects models were used to assess the relationship between seedling and sapling relative density for ten tree species (Table 4) and a suite of fixed effect predictor variables (Table 5). An exploratory analysis of the relationship between summer temperature, CTI and site landform type was conducted, with no significant correlations found to account for in model building. Understory size class was included as a predictor variable to test for any significant differences in relative understory abundance between seedlings and saplings of each tree species. Site number was

included as a random effect in model fitting to control for potential non-independence among study sites (Harrison et al., 2018). Given the proportional nature of our response variables, with values ranging from 0 to 1, arcsine square root transformations were performed to stabilize the variance at the low and high ends of the distributions (Sokal & Rohlf, 1995).

Table 4: Boreal and northern temperate tree species included in linear mixed-effects modeling.

Species	Biome	Leaf-Type
Balsam fir	Boreal	Conifer
Black spruce	Boreal	Conifer
Northern red oak	Northern temperate	Broadleaf
Northern white cedar	Northern temperate	Conifer
Paper birch	Boreal	Broadleaf
Quaking aspen	Boreal	Broadleaf
Red maple	Northern temperate	Broadleaf
Red pine	Northern temperate	Conifer
White pine	Northern temperate	Conifer
White spruce	Boreal	Conifer

Table 5: Description of environmental variables assessed in examining relative understory abundance of ten boreal and temperate tree species across the BWCAW. Climate date derived from HOBO hourly HOBO measurements described in the methods. Tree species included in Boreal RBA are balsam fir, jack pine, paper birch, quaking aspen and white spruce.

Variable	Units	Description
Size Class	Seedling/Sapling	Understory regeneration size class
Conspecific RBA	#	Relative overstory basal area of conspecific tree species
Boreal RBA	#	Relative overstory basal area of boreal tree species
Worm Invasion	#	IERAT ranking on a 1-5 scale
STmax	°C	Average site maximum summer (JJA) temperature
STmin	°C	Average site minimum summer (JJA) temperature
STavg	°C	Average site summer (JJA) temperature
WTmax	°C	Average site maximum winter (DJF) temperature
WTmin	°C	Average site minimum winter (DJF) temperature
WTavg	°C	Average site winter (DJF) temperature
CTI	#	Compound topographic index

Model building for each tree species followed an iterative process using the authors' domain knowledge and tests of statistical significance to guide final model selection. A full model using all single predictor variables was first fit, using only data from sites where the response variable species was present in the understory and/or overstory (Fig 26). From there, several two-way interactions were tested for inclusion in the full model based on whether their inclusion resulted in significant reductions in Akaike's Information Criterion (AIC) at a p-value of 0.05. Fixed effect variables (excluding lower order interaction terms) were then tested for removal from the full model using a backward stepwise process until no further significant reductions in AIC were achieved. All model fitting was performed using the lme4 package (version 1.1-18-1) in R (Bates et al., 2015, R Development Core Team, 2018).

Results

Ten tree species were found in the understory and/or overstory at a sufficient number of study sites to support model building (Table 4). Six additional tree species were encountered in the understory and/or overstory of at least one study site, but were not included in analyses due to insufficient sample sizes. These species included American mountain ash (*Sorbus americana*), big-tooth aspen (*Populus grandidentata*), black ash (*Fraxinus nigra*), sugar maple (*Acer saccharum*), tamarack (*Larix laricina*), and yellow birch.

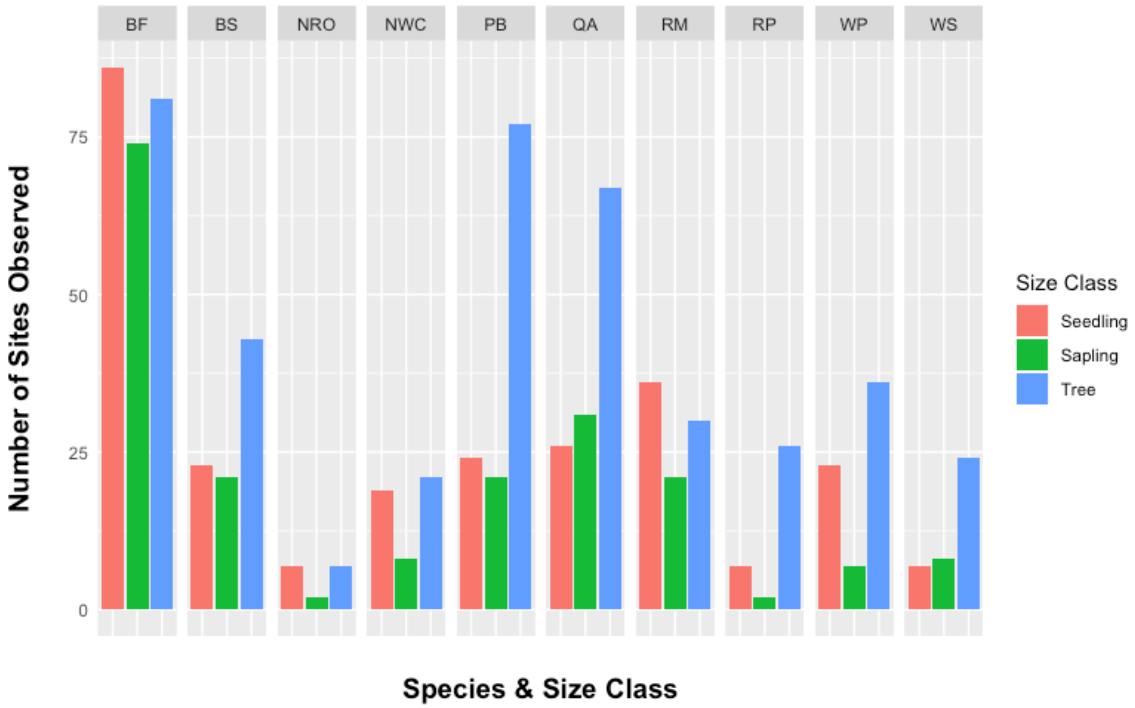


Figure 26: Study site frequency by species and size class (n=106). BF=Balsam fir, BS=Black spruce, NRO=Northern red oak, NWC=Northern white cedar, PB=Paper birch, QA=Quaking aspen, RM=Red maple, RP=Red pine, WP=White pine, WS=White spruce.

Modeling results indicate species-specific shifts in seedling, sapling and combined seedling and sapling regeneration performance in response to changes in temperature, earthworm invasion and CTI, which was a proxy for soil moisture availability in our study, within and across boreal and northern temperate species groupings. Summer temperature predictor variables were included in the top performing models for nine of ten species, including significant interactions with size class, IERAT ranking, CTI and relative overstory basal area of boreal species. Earthworm invasion ranking was included in the top performing models for six of ten species, with three of those species showing a significant interaction between earthworm invasion and average, maximum and minimum summer temperature respectively. CTI was included in the top performing models for four of ten species, with three species showing a significant interaction between CTI and average, maximum and minimum summer temperature

respectively. Relative overstory basal area of boreal species was included in the top performing models for seven of ten species, exhibiting a primarily positive relationship with the relative understory abundance of individual boreal species. Significant differences in seedling versus sapling understory relatively densities were found for five of ten species. Model performances ranged from poor (i.e., paper birch, R2m=0.08) to good (i.e., northern red oak, R2m=0.85), with most models performing adequately (Table 6).

Table 6: Fixed effect parameter estimates and standard errors for best performing linear mixed-effects models of species understory relative density, with site as a random effect. BF=Balsam fir, BS=Black spruce, NRO=Northern red oak, PB=Paper birch, QA=Quaking aspen, RM=Red maple, RP=Red pine, WP=White pine, WS=White spruce.

Coefficient	BF	BS	NRO	NWC	PB	QA	RM	RP	WP	WS
Intercept	5.83 (1.51)	-9.44 (2.66)	0.07 (0.03)	1.12 (1.26)	-0.71 (0.41)	-0.69 (1.09)	-3.5 (2.24)	-0.67 (0.88)	-1.71 (1.02)	-3.54 (4.3)
Size Class (seedling)				0.17 (0.04)		-0.15 (0.05)	0.29 (0.08)	0.16 (0.07)	-1.5 (0.46)	
Conspecific RBA	0.62 (0.27)	0.87 (0.19)	0.73 (0.08)	0.24 (0.25)					-0.05 (0.08)	1.87 (0.38)
Boreal RBA		4.12 (1.78)		0.52 (0.21)	0.09 (0.06)	0.27 (0.1)	-0.19 (0.14)		2.05 (1.16)	-8.2 (1.63)
STavg	-0.67 (0.19)	0.19 (0.11)		-0.09 (0.12)	0.07 (0.03)	0.16 (0.05)	0.35 (0.14)	0.35 (0.13)	0.04 (0.05)	0.88 (0.29)
STmax	0.19 (0.07)	0.22 (0.07)						-0.13 (0.05)		-0.29 (0.12)
STmin	0.31 (0.12)			0.03 (0.11)	-0.03 (0.03)	-0.07 (0.06)	-0.32 (0.11)	-0.21 (0.07)	0.01 (0.04)	-0.60 (0.21)
WTavg	0.59 (0.26)	0.17 (0.08)				0.08 (0.03)	-0.23 (0.07)			-1.05 (0.31)
WTmax	-0.26 (0.1)	-0.16 (0.07)					0.14 (0.07)		0.07 (0.02)	0.30 (0.08)
WTmin	-0.22 (0.14)	-0.11 (0.03)							-0.09 (0.03)	0.51 (0.18)
IERAT Rank 2		2.41 (1.9)		0.1 (0.15)		0.48 (0.83)	-0.43 (0.22)	0.15 (0.12)		3.79 (2.76)
IERAT Rank 3		4.63 (4.17)		0.08 (0.13)		-0.54 (1.18)	-0.54 (0.24)	0.33 (0.16)		1.08 (2.39)
IERAT Rank 4		15.48 (4.68)		-0.5 (0.21)		-3.94 (1.74)	-0.71 (0.28)	1.00 (0.23)		10.82 (4.27)
IERAT Rank 5				-0.19 (0.28)		-10.09 (3.37)		0.13 (0.22)		29.16 (19.18)
CTI	0.43 (0.2)			-0.69 (0.15)	-0.01 (0.01)					0.49 (0.13)
Size Class									0.13 (0.04)	
STavg:IERAT Rank 2		-0.15 (0.11)								
STavg:IERAT Rank 3		-0.27 (0.24)								
STavg:IERAT Rank 4		-0.88 (0.27)								
STmax:IERAT Rank 2										-0.15 (0.11)
STmax:IERAT Rank 3										-0.03 (01)
STmax:IERAT Rank 4										-0.44 (0.17)
STmax:IERAT Rank 5										-1.21 (0.79)
STmin:IERAT Rank 2						-0.04 (0.07)				
STmin:IERAT Rank 3						0.05 (0.1)				
STmin:IERAT Rank 4						0.32 (0.14)				
STmin:IERAT Rank 5						0.86 (0.28)				
BorealRBA:STavg									-0.12 (0.07)	
BorealRBA:STmax		-0.18 (0.07)								0.33 (0.07)
STavg:CTI	-0.03 (0.01)									
STmax:CTI										-0.02 (0.01)
STmin:CTI				0.06 (0.01)						
R2m	.27	.58	.85	.54	.08	.33	.41	.36	.46	.57

Temperature

Average summer temperature was a significant predictor of understory regeneration for nine of ten species (Table 6). Understory seedling and sapling relative densities of balsam fir, northern white cedar and red pine were negatively related to average summer temperature, with balsam fir exhibiting the strongest relationship with the least amount of uncertainty. Understory seedling and sapling relative densities of red maple, eastern white pine, black spruce, paper birch and quaking aspen were positively related to average summer temperature, with red maple exhibiting the steepest gains across both seedlings and saplings (Figure 27). Northern red oak was the only species that did not include a temperature based predictor variable in its final model. We attribute this to a small sample size of sites where NRO was present, all of which were located in the warmer western portion of the study area on similar landform types, thus minimizing site to site temperature variability. The range of average summer temperatures at sites where northern red oak was present was 18.14°C to 19.01°C, compared to mean average summer temperatures of 18.55°C at western sites (Echo Trail and Fernberg Road areas), 17.08°C at eastern sites (Gunflint Trail area) and 17.65°C across all sites.

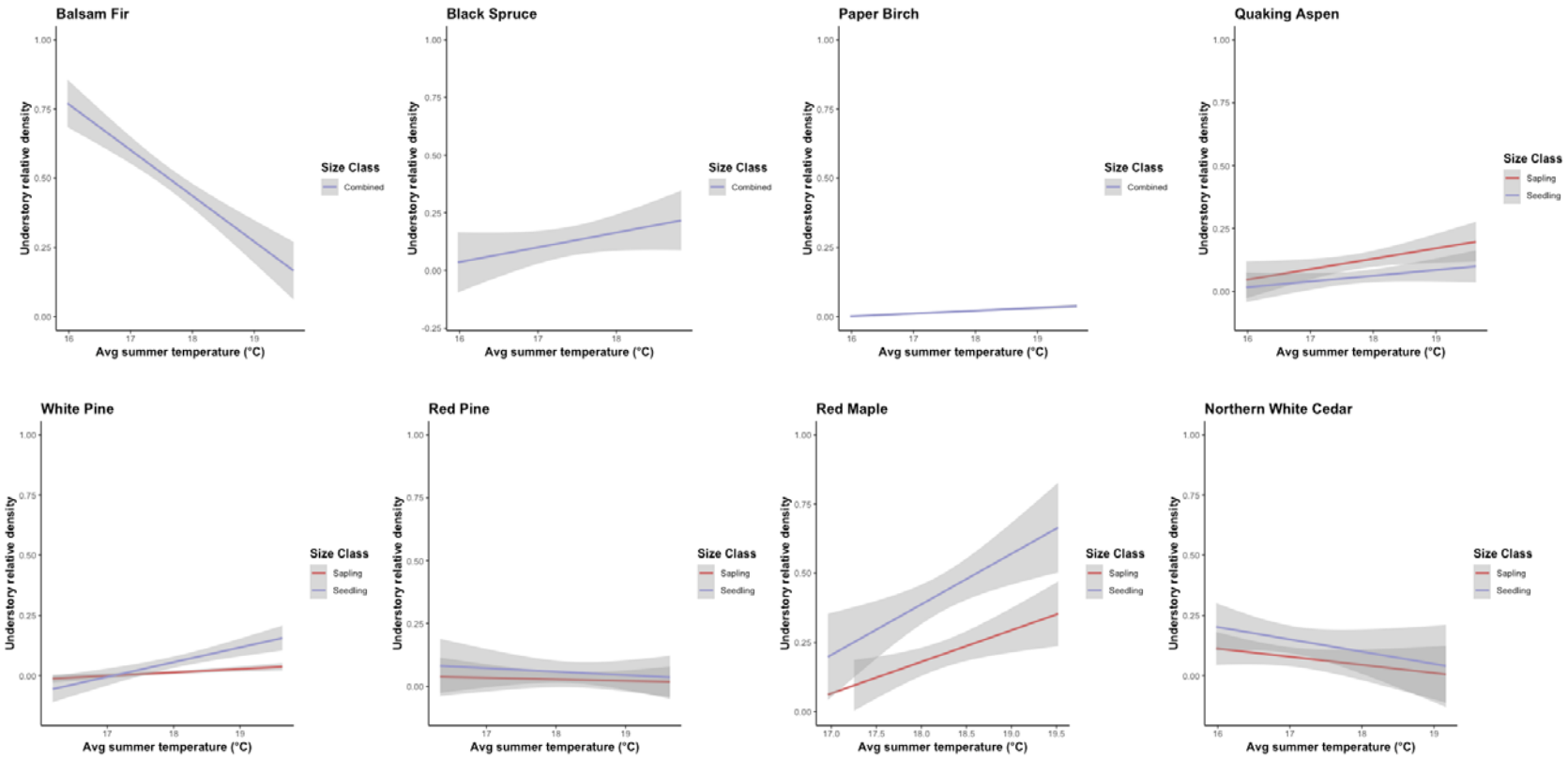


Figure 27: Modeled understory relative density as a function of average summer (JJA) temperature for eight species.

Degree of earthworm invasion

IERAT ranking was also a significant predictor of seedling and sapling relative densities for six of ten species, with significant interactions with summer temperature for four of those six. Understory seedling and sapling relative densities of red maple and northern white cedar were negatively related to IERAT ranking, with saplings of both species affected to a greater degree than seedlings. Red maple exhibited a stronger negative relationship with IERAT ranking than did northern white cedar, and with a lower level of uncertainty. Understory seedling and sapling relative density of red pine was positively related to IERAT ranking, with seedlings affected to a greater degree than saplings. At cool sites, understory seedling and sapling relative density of black spruce was positively related to IERAT ranking, while at warm sites, the relationship was negative. At both cool and warm sites, understory seedling and sapling relative density of quaking aspen and white spruce was positively related to IERAT ranking (Figure 28).

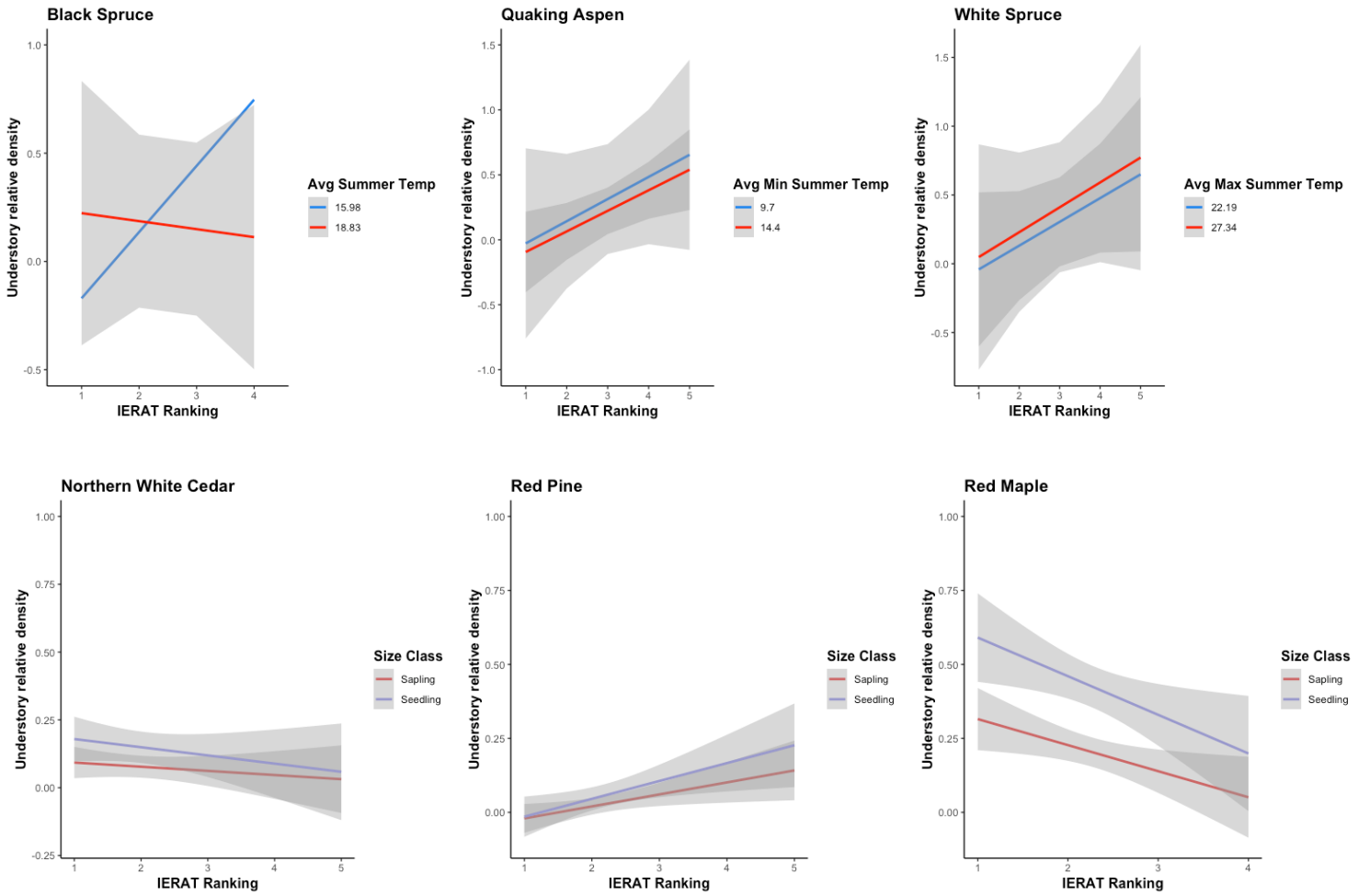


Figure 28: Modeled understory relative density as a function of IERAT ranking and temperature interactions where applicable.

Compound topographic index (CTI)

Three species exhibited a significant interaction between CTI and summer temperature. At cool sites, understory seedling and sapling relative density of balsam fir was negatively related to CTI. Conversely, at warm sites, the relationship was positive, reaching a point of convergence with cool sites at a maximum CTI value of approximately eight. At cool and warm sites, understory seedling and sapling relatively density of white spruce was positively related to CTI, with warm sites exhibiting a stronger relationship than cool sites. At cool sites, understory seedling and sapling relative density of northern white cedar was negatively related to CTI. Conversely, at warm sites, the relationship was positive, with a point of convergence at an approximate CTI value of 0 (Figure 29).

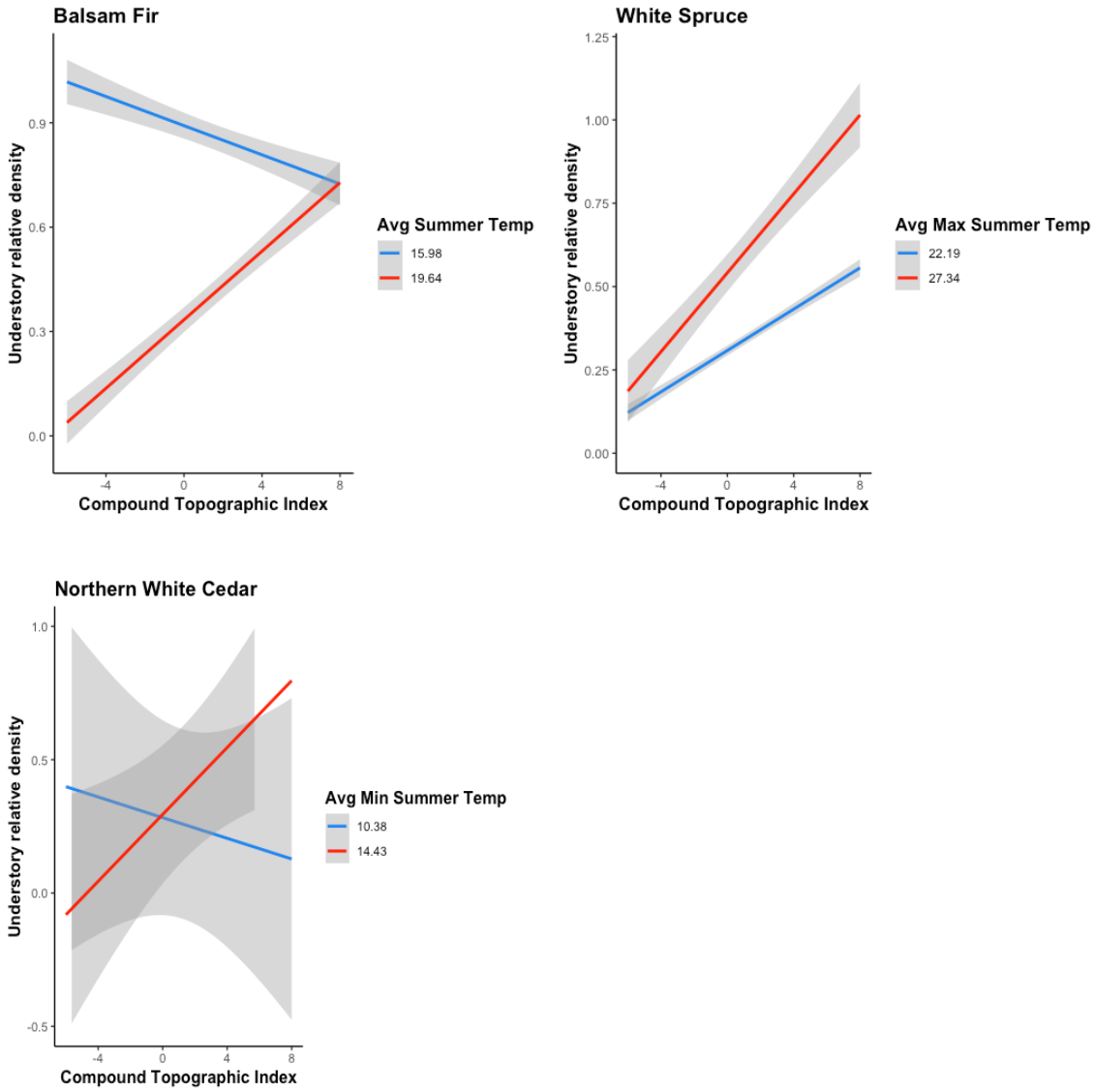


Figure 29: Modeled understory relative density as a function of CTI and temperature interactions where applicable.

Relative basal area of boreal species (Boreal RBA)

Relative seedling and sapling densities of northern white cedar, quaking aspen and paper birch were all positively related to Boreal RBA, while red maple was negatively related. Three species exhibited a significant interaction between relative basal area of boreal species and summer temperature. At both cool and warm sites, understory seedling and sapling relative density of black spruce was negatively related to Boreal RBA, with warm sites exhibiting a relationship of significantly greater magnitude. At both cool and warm sites, understory seedling and sapling relative density of white spruce was negatively related to Boreal RBA, with warm sites exhibiting a relationship of slightly greater magnitude. At cool sites, understory seedling and sapling relative density of white pine was positively related to Boreal RBA. At warm sites, the relationship was negative, converging at an approximate Boreal RBA value of 0.4 (Figure 30).

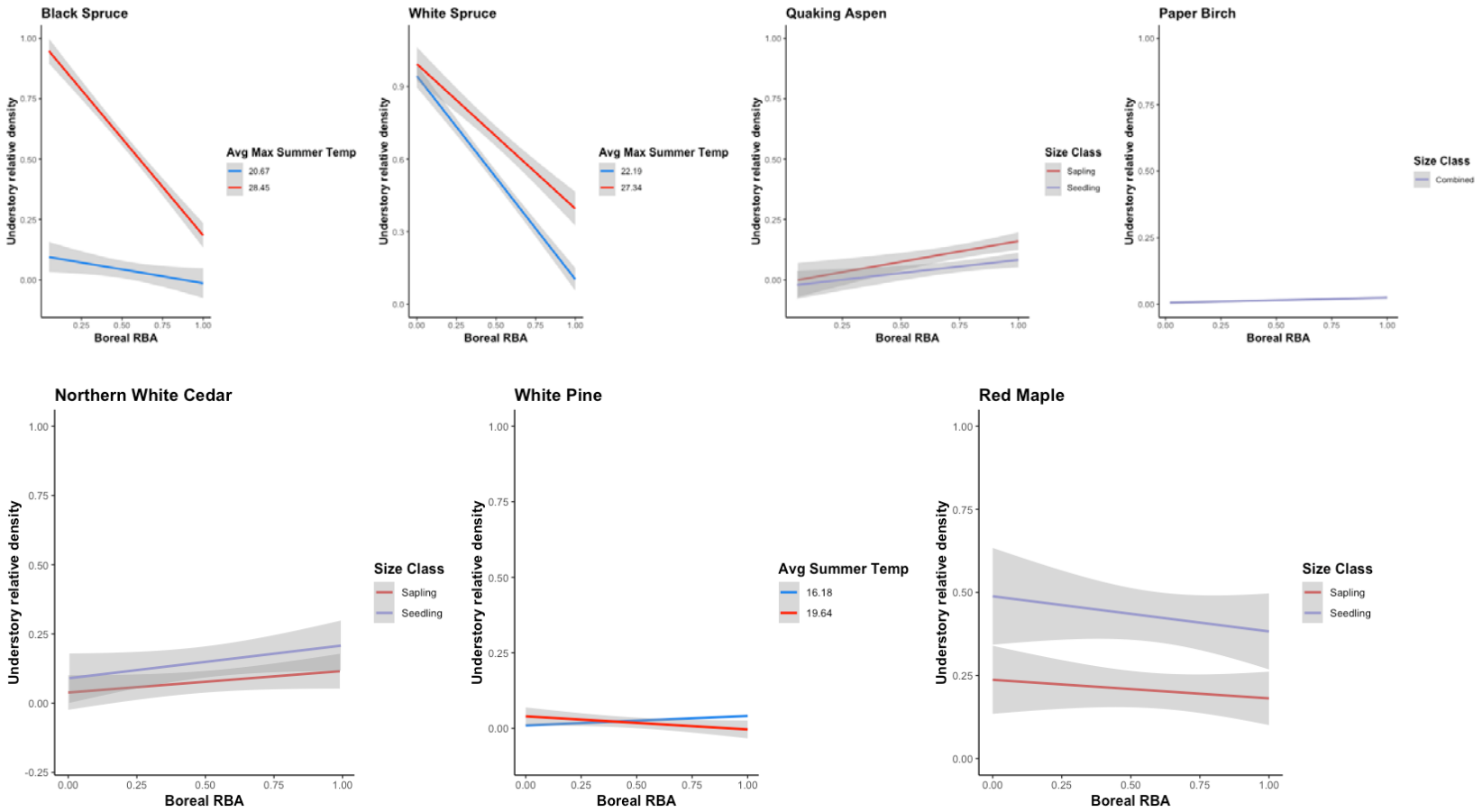


Figure 30: Modeled understory relative density as a function of Boreal RBA and temperature interactions where applicable

Discussion

To aid future climate-change adaptation planning efforts for the BWCAW, we sought to understand how temperature, overstory composition, soil moisture potential and earthworm invasion are currently affecting the relative understory abundance of boreal and temperate tree species in the forests of the BWCAW. We hypothesized that: 1) higher average summer temperatures would be negatively related to relative understory abundance of boreal species and positively related for temperate species, 2) increased soil moisture potential would be positively related to relative understory abundance of boreal species, and 3) degree of earthworm invasion would be positively related to relative understory abundance of boreal species and negatively related for temperate species. Our results indicate that summer temperature is a key driver of relative differences in boreal and northern temperate understory regeneration across the mixed-boreal forests of the BWCAW. However, they also indicate that multiple interrelated variables relating to overstory and understory conditions must also be accounted for in understanding a more complete picture of tree regeneration trends at finer spatial scales, and in designing climate change adaptation plans for the BWCAW.

Summer temperate had mixed effects on the relative understory densities of northern temperate tree species. As expected, red maple seedling and sapling relatively densities were positively related with increasing summer temperatures, with seedling relative density increasing more steeply. Compared to red maple, which is more widespread throughout the BWCAW, the spatial distribution of northern red oak is limited to the western side of the wilderness, where average summer temperatures are at their highest. Mean average summer temperature at sites where northern red oak was

present was 18.58°C, which was approximately 1.5°C and 1.0°C higher than the mean average summer temperature of eastern study sites and all study sites respectively. Northern red oak's limited distribution in the warmer western portion of the wilderness thus masked a strong positive relationship between higher summer temperatures and the relative understory abundance of both seedlings and saplings. Eastern white pine seedling and sapling relatively densities were also positively related to average summer temperature, with seedling relative density increasing more steeply.

Northern white cedar seedling and sapling relative densities were negatively related to average summer temperature, which we suspect may be more a function of soil moisture availability than a physiological response to temperature alone. Northern white cedar seedling establishment is limited to sites with consistent soil moisture, with drought being a major cause of seedling mortality (Curtis, 1959; Johnston and William, 1990). Consistent with these regenerative traits, we found a positive relationship between northern white cedar seedling and sapling relative density and CTI at warmer sites (Figure 29). Red pine seedling and sapling relatively densities were also negatively related to average summer temperature, although more modestly and with a higher degree of uncertainty.

Relative understory seedling and sapling densities of boreal tree species in response to summer temperature was also mixed. As expected, balsam fir seedling and sapling relatively densities were strongly negatively related to summer temperature. Our results are consistent with other empirical studies and support modeled predictions of significant balsam firm declines in the BWCAW and surrounding region under climate change (Swanston et al., 2018; Reich et al., 2015, Duveneck et al., 2014; Fisichelli et al.,

2013; Ravenscroft et al., 2010; Xu et al., 2010; Galatowitsch et al., 2009; Iverson and Prasad, 2007; Walker et al., 2002). However, we did find a positive relationship between balsam fir seedling and sapling relative density and CTI at warm sites, possibly indicating some potential for consistent soil moisture availability to ameliorate the effects of future warmer temperatures for that species (Figure 29).

Black spruce, paper birch and quaking aspen seedling and sapling relative densities were all positively related to average summer temperature (Fig 27). While these results appear counterintuitive, they are placed into context when considering the spatial distribution of each species across our study area, logging history in the BWCAW and recent changes in the natural disturbance regime. Black spruce, paper birch and quaking aspen are three of the most abundant and widely distributed tree species in the BWCAW. Populations of all three species fully span the existing 2°C west to east summer temperature gradient, tempering the effect of temperature in model building. Greater historical logging history in the western BWCAW has led to more second growth, aspen and birch forests on the warmer side of the wilderness. And over the past century, fire suppression and land fragmentation to the south have lengthened fire recurrence intervals in the BWCAW to greater than 700 years (Frelich 2002), possibly allowing shade-tolerant balsam fir seedlings and saplings to outcompete quaking aspen, paper birch and black spruce on the cooler, eastern side of the wilderness despite ample seed sources.

Supporting evidence for this latter point can be found in the positive relationship between quaking aspen and black spruce seedling and sapling relative densities and IERAT ranking at cooler eastern sites (Fig 28). In removing the humus (O_a) layer and creating a bare mineral soil surface, earthworms create seedbed conditions similar to

recently burned sites conducive to regeneration by species that are better able to germinate and survive on bare mineral soil surfaces. These include quaking aspen, black spruce, white spruce and red pine, all of which exhibited positive relationships between seedling and sapling relative density and IERAT ranking (Figure 28). While red maple is also able to germinate on bare mineral soil surface, it exhibited a clear negative relationship with IERAT ranking in our study. Northern white cedar also exhibited a negative relationship with IERAT ranking, possibly related to the drier seedbed conditions created by earthworms (Frelich et al., 2006). These findings are consistent with other studies that have predicted earthworm invasion may favor boreal tree species resistance over northern temperate tree expansion in the short-term under climate change (Fisichelli et al, 2013, Fisichelli et al., 2012, Frelich et al., 2012). However, they also highlight a potential lack of advance boreal species regeneration beyond balsam fir in the cooler eastern BWCAW, where boreal species may be most likely to find microrefugia depending on the pace and extent of future climate change.

Relative understory seedling and sapling densities of boreal and northern temperate tree species in response to Boreal RBA was mixed, with confounding results between the two groupings (Fig 30). While the relative density of quaking aspen and paper birch regeneration exhibited a strong positive relationship with Boreal RBA, the inverse was true of black and white spruce. Red maple seedling and sapling relative density declined with increasing Boreal RBA, while the inverse was true for northern white cedar. Fisichelli et al., successfully used Boreal RBA as a measure of temperate expansion into adjacent boreal forest patches, however the geographic range of their climate and temperate-boreal forest gradient was significantly larger than our study

(Fisichelli et al., 2013). In conducting a simple linear regression against Boreal RBA, we found just two significant predictor variables; average minimum summer temperature, which was negatively related, and IERAT ranking, which was positively related, with our predictive model returning an r squared of 0.26. We suspect that our confounding results with regards to Boreal RBA are due more to our limited climate and boreal-temperate gradient with the BWCAW, and in particular an insufficient number of northern temperate tree dominated sites, rather than any signal of spruce decline at the expense of northern temperate tree species. Boreal RBA in our study appears more related to identifying current growing conditions that may be better suited to boreal species, including lower temperatures and mineral soil seedbed conditions resulting from earthworm invasion, however we do not place high confidence in these particular results.

Conclusions

Climate change presents an unprecedented threat to the forests of the BWCAW that will not be mitigated by federal protection (Frelich and Reich, 2009). The boreal tree species that currently dominate the BWCAW landscape, and contribute to its ecological, cultural and recreational values, are projected to retreat to the northeast, potentially out of the wilderness and Minnesota altogether by the end of the century. Given the velocity of future climate change and the unprecedented corresponding rates at which northern temperate tree species would need to migrate to keep pace, it remains unclear if a successful boreal to temperate forest transition will occur. While modeling efforts have been, and will continue to be, critically important in identifying landscape level trends in shifts in suitable habitat for boreal and northern temperate tree species in the BWCAW, future management decisions designed to "protect and enhance the natural values…of the

wilderness" would benefit from a ground-level understanding of the multitude of interrelated variables influencing tree regeneration trends today, and in the future.

Our results are consistent with other studies in the region in elucidating both the importance of summer temperature, and the interrelated influences of overstory and understory conditions, in determining tree regeneration trends in the mixed-boreal forests of the BWCAW. They are also consistent with other regional studies in identifying conditions such as earthworm invasion and sites with consistent soil moisture availability as means to support the short-term resistance of boreal tree species in the wilderness, and possibly identify sites able to support long-term hold-out populations of boreal tree species in small microrefugia under a future warmer and drier climate (Frelich et al. 2012, Hannah et al., 2014). For example, our results indicate a retreat to wetter sites by boreal fir and north temperate cedar at the warm end of the temperature gradient and increased regeneration of black spruce, quaking aspen and paper birch at earthworm invaded sites. Further studies that are able to model summer temperature, soil moisture, cold-air pooling and earthworm invasion at fine spatial resolution across the landscape would be beneficial in this regard.

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